KISTER

THE LIVING UNIVERSE
An Encyclopaedia of
the Biological Sciences

The animal world

~~444~~
~~4178~~

4006
7.5.87

~~3406~~
~~7.5.87~~

STATE INSTITUTE OF EDUCATION
BANIPUR

~~A/17~~

~~402~~

4008

The animal world

STATE INSTITUTE OF EDUCATION ★ BANIPUR

S.C.E.R.T., West Bengal
Library
Calcutta
25/3, B. C. Road

THE LIVING UNIVERSE : AN ENCYCLOPAEDIA OF THE BIOLOGICAL SCIENCES

THE LIVING UNIVERSE

An Encyclopaedia of the Biological Sciences

S.C.E.R.T., West Bengal
Date 7-5-87
Acc. No. 4006

L'UNIVERS ANIMAL
La Vie et L'Homme, Encyclopédie des Sciences Biologiques
© 1961 by Éditions René Kister, Geneva.
All rights reserved.

English Edition © 1964 by Thomas Nelson and Sons Ltd
36 Park Street London W1
Parkside Works Edinburgh 9
117 Latrobe Street Melbourne C1
10 Warehouse Road Apapa Lagos

Thomas Nelson and Sons (Africa) (Pty) Ltd
P.O. Box 9881 Johannesburg

Thomas Nelson and Sons (Canada) Ltd
81 Curlew Drive Don Mills Ontario

Thomas Nelson and Sons
Copewood and Davis Streets Camden 3 NJ

Société Française d'Éditions Nelson
97 rue Monge Paris 5

Printed in Spain

The animal world

STATE INSTITUTE OF EDUCATION
BANIPUR

NELSON

The animal world is an abundance of species, a multitude of structures, and an infinite diversity of forms. This variety is found again in the modes of life that permit animals to become adapted to the strangest environments, and we also meet it in the multifarious devices that life makes use of to propagate itself.

THE LIVING UNIVERSE

An Encyclopaedia of the Biological Sciences

SCIENTIFIC EDITORS

Rémy CHAUVIN
Director of Research, French National Institute of Agronomy

Pierre CHOUARD
Professor at the Sorbonne

Albert DELAUNAY
Head of the Department of Experimental Pathology, Institut Pasteur

Romolo DEOTTO
Director of the Institute of Microbiology, University of Milan

Claude JACQUILLAT
of the Hôpitaux de Paris

Raoul KOURILSKY
Professor of the Faculty of Medicine, Paris

Paul LAGET
of the University of Paris

Alexandre M. MONNIER
Professor at the Sorbonne

Jean Paul NITSCH
Deputy-Director of the Phytotron, CNRS, France

Jean ROSTAND
of the French Academy

Philippe SENGEL
Deputy-Director of the Embryology Laboratory, Collège de France

Etienne WOLFF
Professor at the Collège de France

SCIENTIFIC EDITOR OF THE SERIES Albert DELAUNAY

ARTISTIC EDITOR OF THE SERIES Hans ERNI

This series is published under the general supervision of Herman GREGOIRE *in collaboration with* Paul ALEXANDRE, *literary editor. The work was originated by* Herman GREGOIRE *and* Pierre KISTER. *Technical and photographic services by* Lucien LOUVEGNIES.

The animal world

This volume of THE LIVING UNIVERSE, *An Encyclopaedia of the Biological Sciences, has been produced under the direction of* Rémy CHAUVIN, *in collaboration with Professor* Jean G. BAER, *University of Neuchatel;* Lloyd BEIDLER, *Professor of Physiology, Florida State University, Tallahassee, U.S.A.;* Pierre C. BLIN, *Professor of Anatomy, National Veterinary School, Toulouse, France;* Robert A. BUTLER, *Ph.D., University of Chicago; Professor* André de CAYEUX *of the Sorbonne;* Claude DELAMARE-DEBOUTTEVILLE, *Deputy Director of the Arago Laboratory, Banyuls, France;* Michel DELSOL, *Professor of Biology, Catholic University of Lyons, France;* C. H. FRASER ROWELL, *M.A., Ph.D., University of Cambridge;* Karl GÖSSWALD, *Director of the Institute of Applied Zoology, University of Wurzburg;* Pierre P. GRASSÉ *of the French Academy of Sciences; Dr.* Pierre GRISON, *Director of the Laboratoire de Lutte biologique et de Biocoenotique, La Minière, France;* Otto KOEHLER, *Professor of Zoology, University of Freiburg;* Jacques LECOMTE, *French National Institute of Agronomy, Bures-sur-Yvette, France;* Martin LINDAUER, *Institute of Zoology, University of Munich; Dr.* Jean LOUVEAUX, *French National Institute of Agronomy, Bures-sur-Yvette, France; Professor* Raoul M. MAY *of the Faculty of Sciences, Paris;* Desmond MORRIS, *Curator of Mammals, Zoological Society, London; Professor* Paul PESSON, *Institut National Agronomique, Paris;* Bernard RICHARD, *Laboratoire d'Evolution des Etres organisés, Paris; Professor* Leendert de RUITER, *Zoology Laboratory, State University of Groningen, Holland;* Michel SABOURDY, *Centre National de la Recherche Scientifique, Gif-sur-Yvette, France;* Martin W. SCHEIN, *Sc.D., Associate Professor of Animal Behaviour, Pennsylvania State University, U.S.A.;* Vincent B. WIGGLESWORTH, *C.B.E., M.D., F.R.S., Quick Professor of Biology, University of Cambridge. Dr.* J. A. C. BROWN *assisted in the compilation of the English edition.*

CONTENTS

Rémy Chauvin 9 *Introduction*
Pierre-Paul Grassé 15 *The animal world*

PART ONE ANIMALS AND TIME

André de Cayeux 23 *Outlines of palaeontology*
Michel Delsol 31 *Mechanisms of evolution*
Rémy Chauvin 37 *Musing on evolution*
Vincent B. Wigglesworth 42 *Metamorphosis*
Jacques Lecomte 49 *Animal sexuality*
Claude Delamare-Deboutteville 53 *The study of extreme environments*
Raoul M. May 59 *Resistance to death*

PART TWO THE WORLD AS SEEN BY ANIMALS

Hugh Fraser Rowell 65 *The senses of animals*
Lloyd M. Beidler 71 *Taste and smell in animals*
Desmond Morris 75 *Releasers*
Martin W. Schein 80 *Social hierarchies*
Martin Lindauer 87 *The language of bees*
Otto Koehler 91 *Animal thought*
Robert A. Butler 97 *Curiosity in animals*

PART THREE VIEWS OF ANIMAL LIFE

Jean G. Baer 105 *Parasitism and symbiosis*
Jacques Lecomte 109 *The migration of animals*
Rémy Chauvin 113 *The social insects*
Leendert de Ruiter 119 *Camouflage, warning and disguise*
Jean Louveaux 127 *The great symbiosis*

PART FOUR ANIMALS AND MEN

Karl Gösswald 135 *The intensive breeding of ants*
Bernard Richard 139 *The training of animals*
Michel Sabourdy 143 *Animals in the laboratory*
Paul Pesson 148 *Chemical war on insects*
Pierre Grison 154 *The biological struggle*

Two wise men were talking to each other on the Hao bridge.

'Look at those shad,' said one, 'see how they twist and turn with delight.'

'You are not a fish,' replied the other, 'so how can you tell what pleases them?'

'You are not me,' answered the first, 'so how can you be sure that I don't know the reason for their happiness?'

'Because I know,' said the second, 'that you are not a fish and therefore you cannot understand them.'

'You are wrong,' retorted the first. 'You ask me how I know what pleases them. Well, I will tell you: I know because I myself am delighted by the water.'

CHINESE LEGEND

When he looks at the animal world man has always tended to regard it in one or other of two contrasting ways. The first is that held by many primitive peoples: that there is no fixed barrier between man and beast, since they believe that every one of their tribes has actually had its origin in the animal which it regards as its totem, and they therefore accept quite literally the descendents of the totem as blood-brothers. Perhaps it was an unconscious extension of this way of thought that led many writers right up to the middle of last century to take an anthropomorphic view of animals, assuming that they felt, suffered, and even thought just as we do. In consequence, animal behaviour appeared to present no special problem.

Opposed to this view was the theory put forward by the French philosopher René Descartes in the seventeenth century, to the general effect that an animal is nothing but a machine in which everything can be explained in terms of simple reflexes and responses. This belief led many of the religiously-inclined to assume that, if this were the case, man must be very remote from such a machine; the more sceptical, however, drew the opposite conclusion—that he must be very close to the animals indeed. For what, they asked, is the human mind but an epiphenomenon superimposed upon a solid foundation of automatic reflexes?

Modern animal psychologists reject both these extreme views. That reflexes play a large part in animal life is undeniable; but that we can explain everything in this way is unacceptable. Equally they refuse to believe that animals are merely lesser men; for in many respects they are genuinely and profoundly different from us. They do not see

THE ANIMAL KINGDOM

SUB-KINGDOM	CLASS	PRINCIPAL TYPE
Single-celled animals		
PROTOZOA	Rhizopoda	*Amoeba*
	Flagellata	*Trypanosome of Sleeping Sickness*
	Ciliata	*Paramecium*
	Sporozoa	*Malaria parasite*
Multi-cellular animals (Metazoa)		
A. ACOELOMATA: the gut is the only body cavity		
PORIFERA	Calcarea	*Sycon*
	Demospongea	*Bath sponge*
COELENTERATA	Hydrozoa	*Hydra*
	Anthozoa	*Sea anemone*
	Scyphozoa	*Jelly-fish*
	Ctenophora	*Venus's girdle*
B. COELOMATA: body cavity apart from gut		
ECHINODERMATA	Crinoidea	*Sea lily*
	Asteroidea	*Starfish*
	Ophuiroidea	*Brittle star*
	Echinoidea	*Sea urchin*
	Holothuroidea	*Sea cucumber*
ANNELIDA (annulate worms)	Polychaeta	*Aphrodite*
	Oligochaeta	*Earthworm*
	Hirudinea	*Leech*
PLATYHELMINTHA (flat-worms)	Turbellaria	*Planaria*
	Trematoda	*Sheep fluke*
	Cestoda	*Ligula*
NEMERTINA	Nemertina	*Lineus*
VERMIDIANS (abernant worms)	Rotifera	*Wheel animalcules*
	Echiurida	*Bonellia*
	Gephyrea	*Sipunculus*
	Bryozoa	*Plumatella*
		Lingula
MOLLUSCA	Amphineura	*Giant chiton*
	Gastropoda	*Murex, slug*
	Scaphopoda	*Tooth shell*
	Lamellibranchiata	*Oyster*
	Cephalopoda	*Octopus*
NEMATHELMINTHA	Gordiacea	*Gordius*
	Nematoda	*Thread-worm*
	Acenthocephala	*Echinorinchus*
ARTHROPODA	Onychophora	*Peripatus*
	Merostoma	*King crab*
	Arachnida	*Spider*
	Crustacea	*Lobster*
	Myriapoda	*Centipede*
	Insecta	*Dragon-fly, termite, beetle, butterfly, fly, bee, grass-hopper, bug*
BRACHIOPODA	Brachiopoda	*Lingula*
PROTOCHORDATA	Cephalochorda	*Amphioxus or lancelet*
	Tunicata	*Botryllus*
VERTEBRATA	Pisces	*Shark, pike, salmon*
	Amphibia	*Salamander, frog*
	Reptilia	*Lizard, tortoise, crocodile*
	Aves	*Eagle, pigeon, swallow, ostrich*
	Mammalia	*Elephant, pig, camel, whale, lion, ant-eater, bat, man*

the world with the same eyes, nor hear with the same ears, but very differently. Naturally they share certain problems with mankind—such as feeding, reproducing themselves, and finding shelter. But they solve them in their own way by a logic which is not ours or by means the seeming cruelty or ingenuity of which often disconcerts us.

We have therefore chosen quite deliberately to pose questions rather than to answer them in order to make the reader aware of what is all too apparent to us: the enigmatic nature of the animal world. As to its origins, it is not so simple as was once believed. To begin with, there is the fact of its extraordinary variety and abundance; for the vast panorama of the animal world reveals to us a wealth of structures which have only begun to be studied seriously within comparatively recent times. That evolution is a fact and that these structures have been modified by the passage of time is certain, but we do not yet know why and how these modifications arose or whether a particular modification signifies progress or regression.

Certain groups of animals have escaped the influence of time and survived for millions of years with an unaltered anatomy. Neither their anatomy nor their physiology seems to differ fundamentally from that of other animals which have either evolved into some other form or disappeared completely.

The infinite variety of structures is demonstrated by ways of life which have become adapted to the strangest environments. There seems to be no problem of existence which life has not been able to solve. Neither heat, extreme cold, nor oil inhibit it; apparent death itself may not be an absolute barrier; for there are astonishing cases of revivification after prolonged exposure to conditions which would seem to render any sort of life impossible.

Life shows the same variety in the many and devious ways by which it reproduces itself. Compared with the strange sexual relationships found elsewhere in the animal world, those of man appear to be little more than a short chapter in an immense saga.

Whilst animals live in the same world as ourselves, they do not perceive it as we do. Depending on the species and the infinite variety of sensory equipment, a host of universes are distinguishable, overlapping each other, yet almost impenetrable. It is not easy to picture the world of the bee, which cannot see red light yet is able to see ultra-violet light, invisible to us, as colour, recognises the polarised light of the sky, and tastes sugar not only with its tongue, but also with its antennae and even with its feet.

Neither do animals see each other as we see them: the male wild duck is no more than a bird with a green neck to the female. If his green feathers are plucked from him, he will be repulsed by all the females he meets, while other males will cease to attack him and instead seek an opportunity to mate with him.

Although animals do not express themselves as we do, they do communicate with one another and animal languages undoubtedly exist. In the simplest instances the language is limited to a series of cries of distress, appeal, or challenge, which act on the same kind of animal in the same way that a cry acts on the nerves of all human beings, in whatever language it is uttered. At the other extreme is the language of the bees' dance with subtleties of 'dialogue' and 'dialects' which are still for the most part a mystery. Some creatures appear to possess a measure of unformulated thought which enables them to solve complex problems. The rat and monkey show elementary powers of abstraction, and *rooks and some parakeets are able to count up to seven, further than many primitive tribesmen. Finally and most striking is the recognition of symbols found in some species of monkey and perhaps even in certain insects.*

It is difficult not to associate the behaviour of some animals, such as the Australian paradise birds, with a primitive aesthetic sense. To take a single example: one species constructs a nest of interwoven plant fibres, decorates the inside wall with plucked flowers, crushes violet berries, makes a plug from other fibres, and plunges it into the dye with which it paints its breast and the walls of the nest—all this to attract the females.

As everyone knows, man has no monopoly of social life and a volume twice the size of this would be inadequate to discuss the elaborate organisation of even the few large insect societies that have been studied in detail.

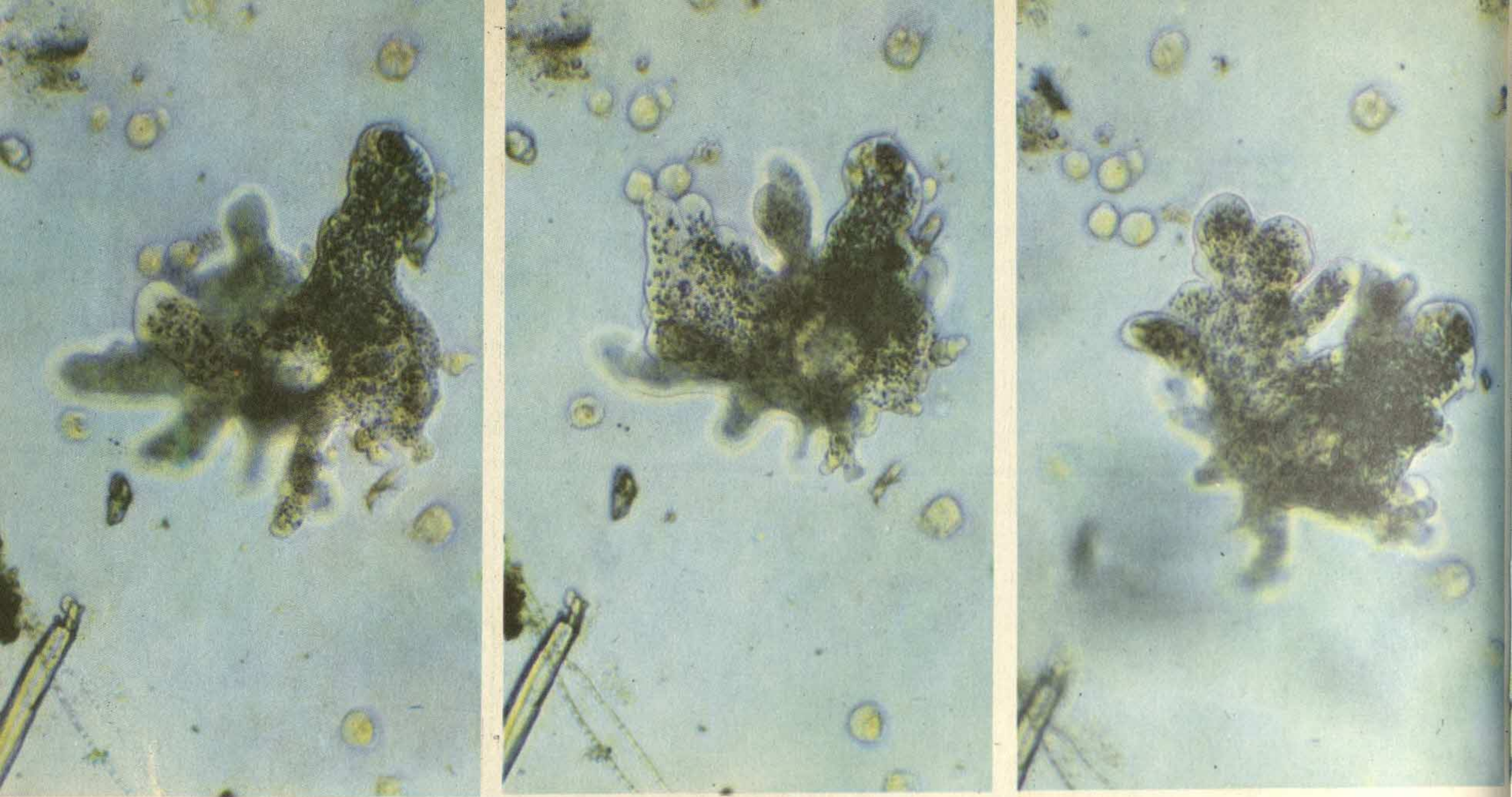
Even more mysterious are such phenomena as migrations, when drives, the nature of which is still unclear, may lead hundreds of millions of migrating animals to their death, and the equally mysterious problems presented by camouflage and mimicry. How, for example, can we explain Kallima, *a butterfly which imitates a dead leaf to perfection in colour, veining, its more or less serrated edges, and even the moulds which attack dead leaves, in such detail that a competent mycologist can easily determine the species of fungus thus imitated? Yet, as has been shown by experiment, a much less detailed imitation of a dead leaf would be adequate to deceive the butterfly's foes. The minute imitations of fungi appear to serve no purpose at all. Why then are they there?*

On the other hand, there are some insects that flaunt their gaudy colours in broad daylight, but are protected from the attacks of birds by their smell or objectionable taste; for when they are fed forcibly to birds the bird spits them out. Taking advantage of this, yet other insects protect themselves by assuming the form and colour of the brazen inedible ones, although very often they belong to quite different species from their model. These insects are not eaten by birds because the bird confuses them with the inedible kind, yet if the mimic insects are crushed so that their characteristic colours no longer show, birds accept them with relish. This case is by no means exceptional and thousands of similar ones could be mentioned.

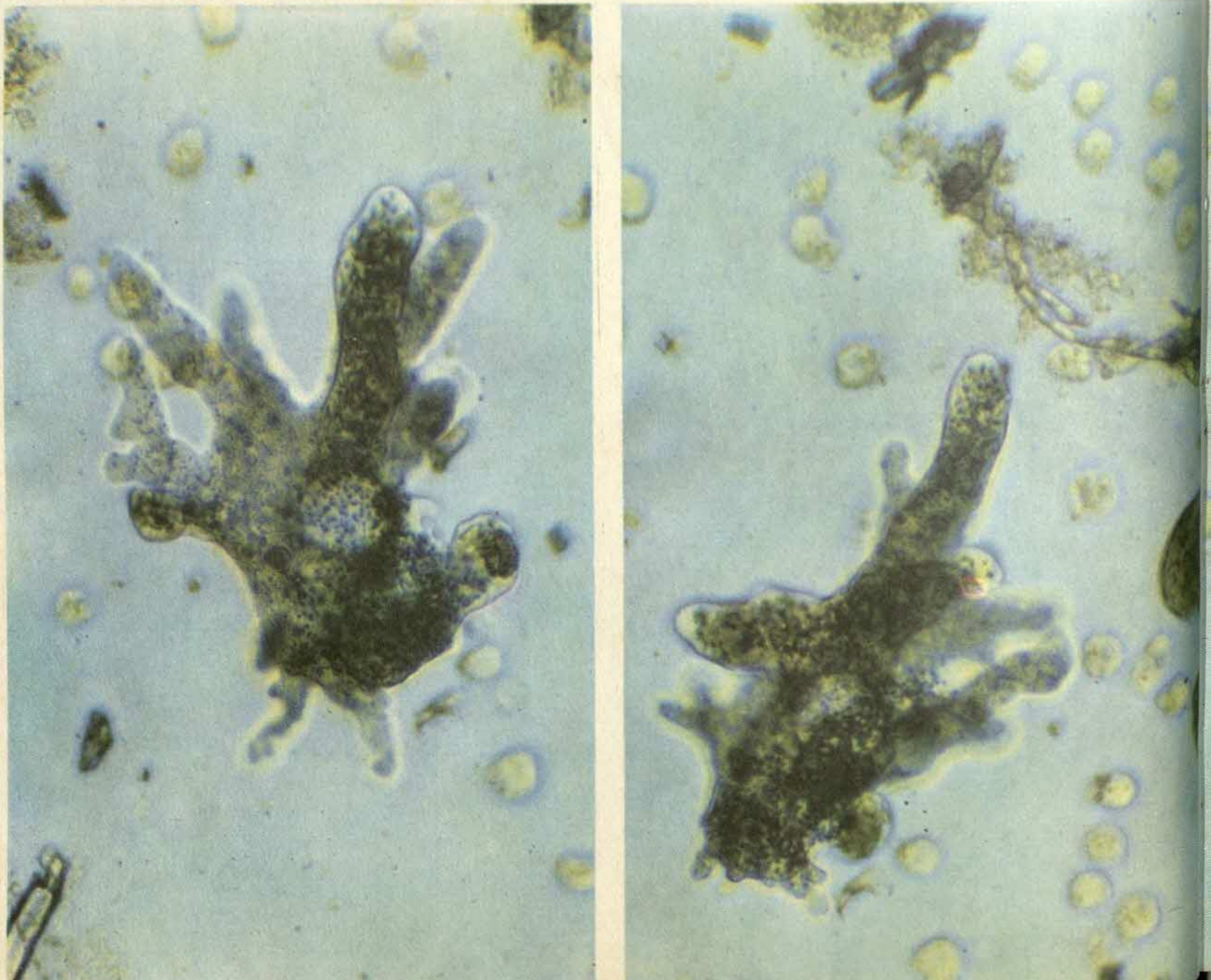
Other problems are presented by the close adaptations found in many cases between the plant and animal world. Thus bees and other insects gather nectar from flowers to make honey, but these visits are also advantageous to many plants which could not otherwise be fertilised. The orchids attract attention in another way. Instead of producing nectar they assume the form and colour of certain female wasps in order to lead the male to attempt to copulate with them. From the wasp's standpoint copulation is naturally ineffectual, but in the course of the male's intrusion, masses of pollen from the orchid stick to its body and these are carried to another flower which is fertilised.

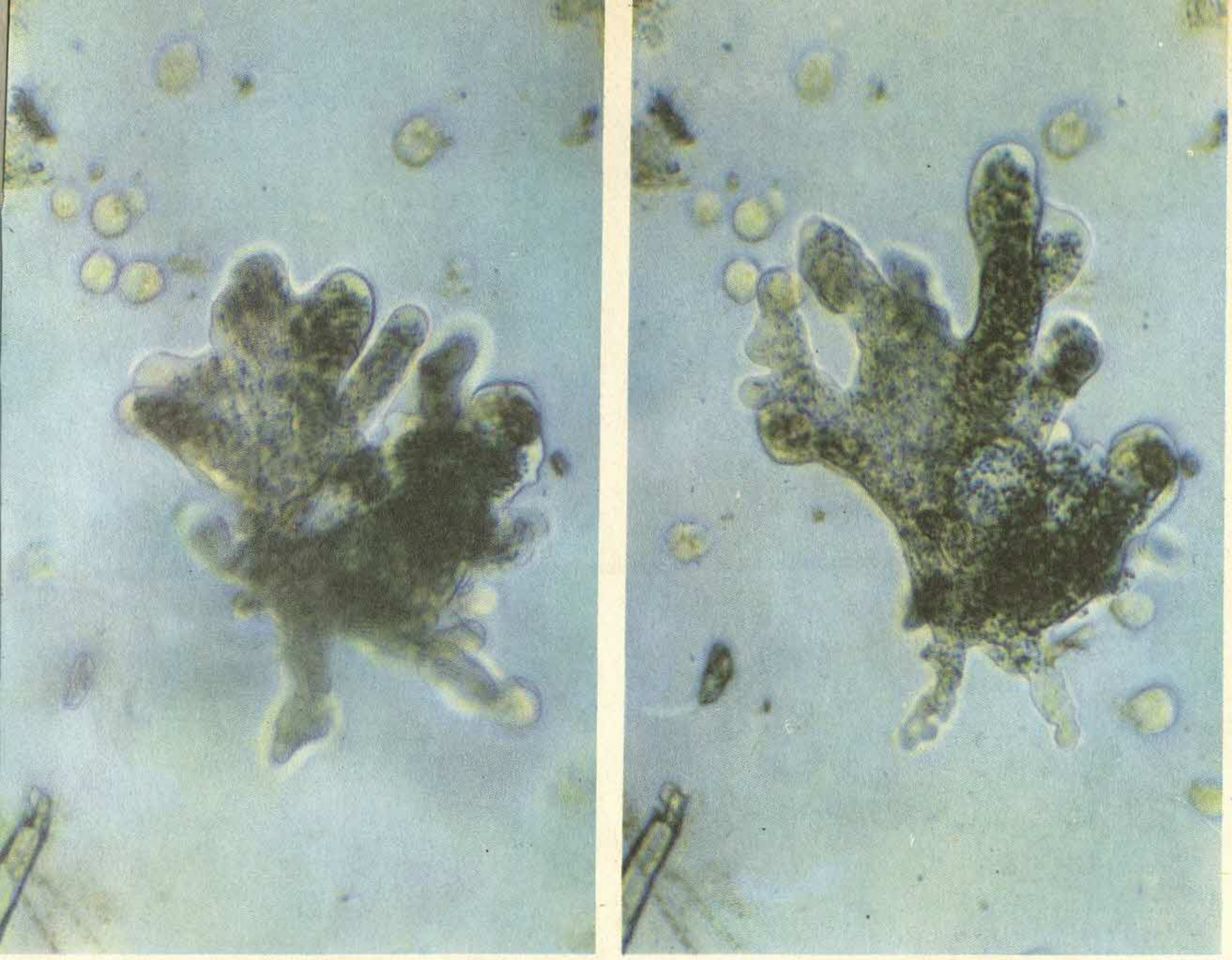
There are many other aspects of living creatures which obviously cannot be discussed in an introduction, but will be dealt with by the eminent biologists who have contributed to this volume. To paraphrase a famous saying: 'Life is like an ocean which beats on our shore, but we have neither ship nor sail with which to explore it.' But if we do not yet have the means to explore far afield, we are well able to acquire them. Science will not always confine itself to the shallows close to the shores of life. Soon, we hope, it will be able to sail towards the open sea.

Rémy CHAUVIN

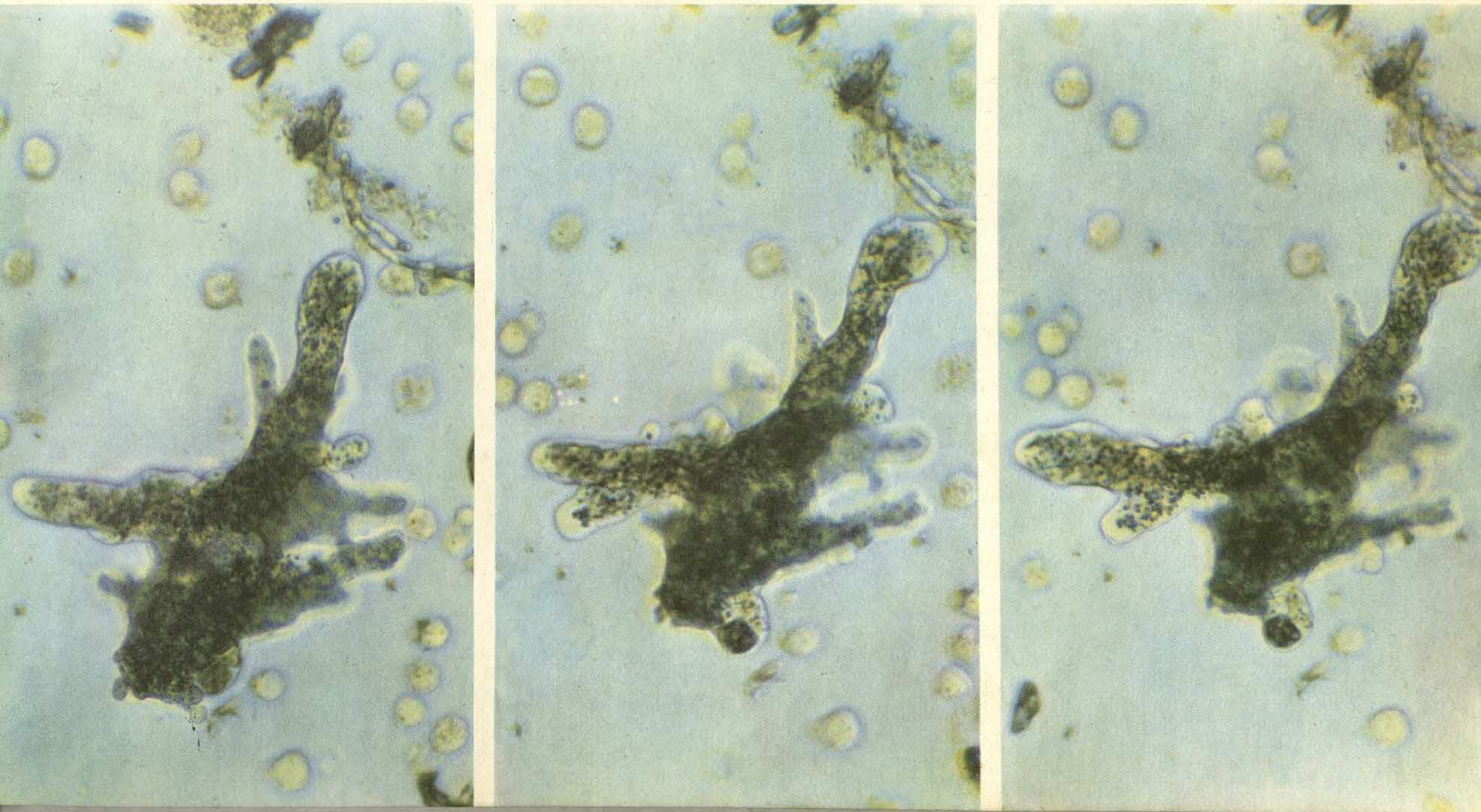


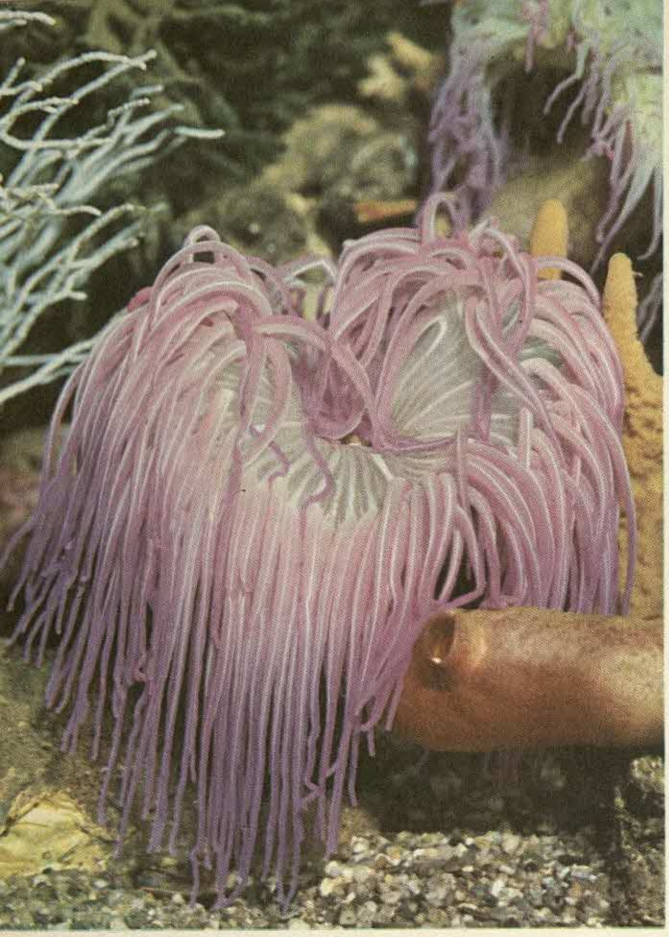
Amoeba moves





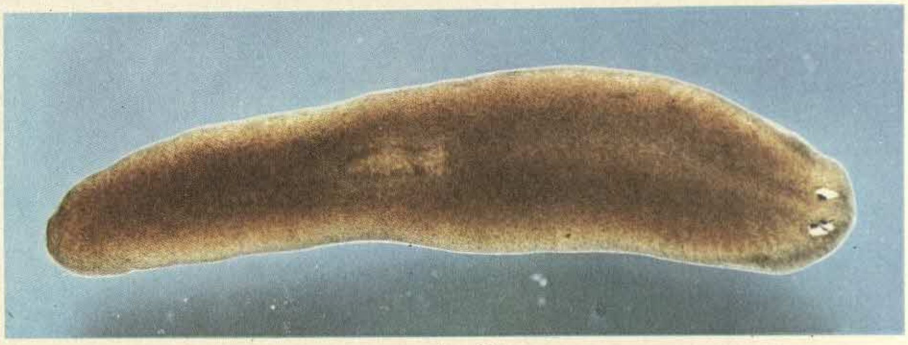
The Amoeba is the prototype of the animal cell. This single cell manifests all the characteristic functions of animal life: nutrition, reproduction, excretion, irritability and motility. Its motility enables it to find food, for it is incapable of assimilating the earth's mineral salts directly, as a plant does. We have described the fundamental mechanism involved in this movement by a series of pictures. Shown here are the long pseudopodia put out by the amoeba, simple projections of protoplasm serving the cell as its locomotory apparatus. The amoeba is making its way towards the top right. During this movement, a cavity in the cytoplasm, a contractile vacuole, which can be seen as a clearer region in the centre, constantly changes shape. As a result of these barely imperceptible changes, the rest of the cell glides forwards towards the pseudopodia, thrust forward by the amoeba to explore its environment or surround its prey. This is the first time that a series of colour photographs has been able to reveal the mechanism of movement in this microscopic creature under a magnifying power strong enough to reveal its internal structure. (Mag. × 650. Photo Lod).





sea anemone

sponge



planarian

snail

sea squirt

The impression that emerges from this collection of invertebrates is one of astonishing variety in form, colour and structure. The zoologist, however, recognises in this coloured fantasia the relationships and increasing complexity of these creatures. The sea anemone, a cylindrical column attached to the rocks, has a crown of predatory tentacles to draw in its prey. The sponge is a digestive sac pierced with numerous pores which absorb its food and reject the waste. The planarian has an excretory network and a primitive nervous system. The snail possesses a lung and has already evolved sense organs. Finally, the sea squirt shows affinities with the vertebrates in having a dorsal cord and gill slits. (Photo Lod).

The animal world

Pierre-P. GRASSÉ

One of the most evident features of life is its diversity: the immense variety of forms and sizes amongst the plants and animals which live in every conceivable environment: forests, prairies, steppes, lakes, rivers, deserts, in the polar regions or deep oceans. Yet only a minute part of the great number of species is visible to the naked eye. The wealth of microscopic creatures far exceeds that of the larger ones that we can see.

At first sight the living world appears chaotic. The giant tree and lowly grass live in the same forest. The humble plankton and the great whale inhabit the same sea.

The early naturalists, faced with this apparent confusion, began to make an inventory in order to classify the fauna and flora of our planet and, although their work began in the sixteenth century it is still far from complete. The discovery of new species proceeds at an ever-increasing rate and there are still no signs that their inventory-making is anywhere near completion. Indeed, the work of classifying species is by no means so simple as might be supposed; for in order to recognise the relationships between species, it is necessary to possess a precise knowledge of anatomy, physiology, genetics, ecology,[1] and geographical distribution.

The scientific classification of living things is based on a system of groups within groups, starting with the most general description and finishing with the most specialised. Each living thing can be put in one of the number of groups. For instance, man belongs to the kingdom Animalia; the phylum or sub-kingdom Chordata (bilaterally symmetrical animals, usually segmented, whose embryos have a tubular nerve cord and a supporting notochord, the rod of closely-packed cells which takes the place of a backbone); the sub-phylum Vertebrate (Chordata having an internal skeleton of cartilage or bone); the *class* Mammalia (warm-blooded vertebrates that suckle their young); the order Primates (Mammalia with long limbs, large five-digit hands and feet, and a highly developed brain); the family Hominidae; the genus, *Homo*; the species, *Homo sapiens*.

Careful research work is required to decide exactly how a particular species should be classified so that we may unravel the long history of living creatures on earth. To biologists, the natural order represents the many devious routes which have been followed by living things before they attained their present form. Clearly, nature would be unintelligible if we were ignorant of the past, for the evolution of plants and animals is the result of a succession of phenomena which never repeat themselves in quite the same way.

Primitive forms of life

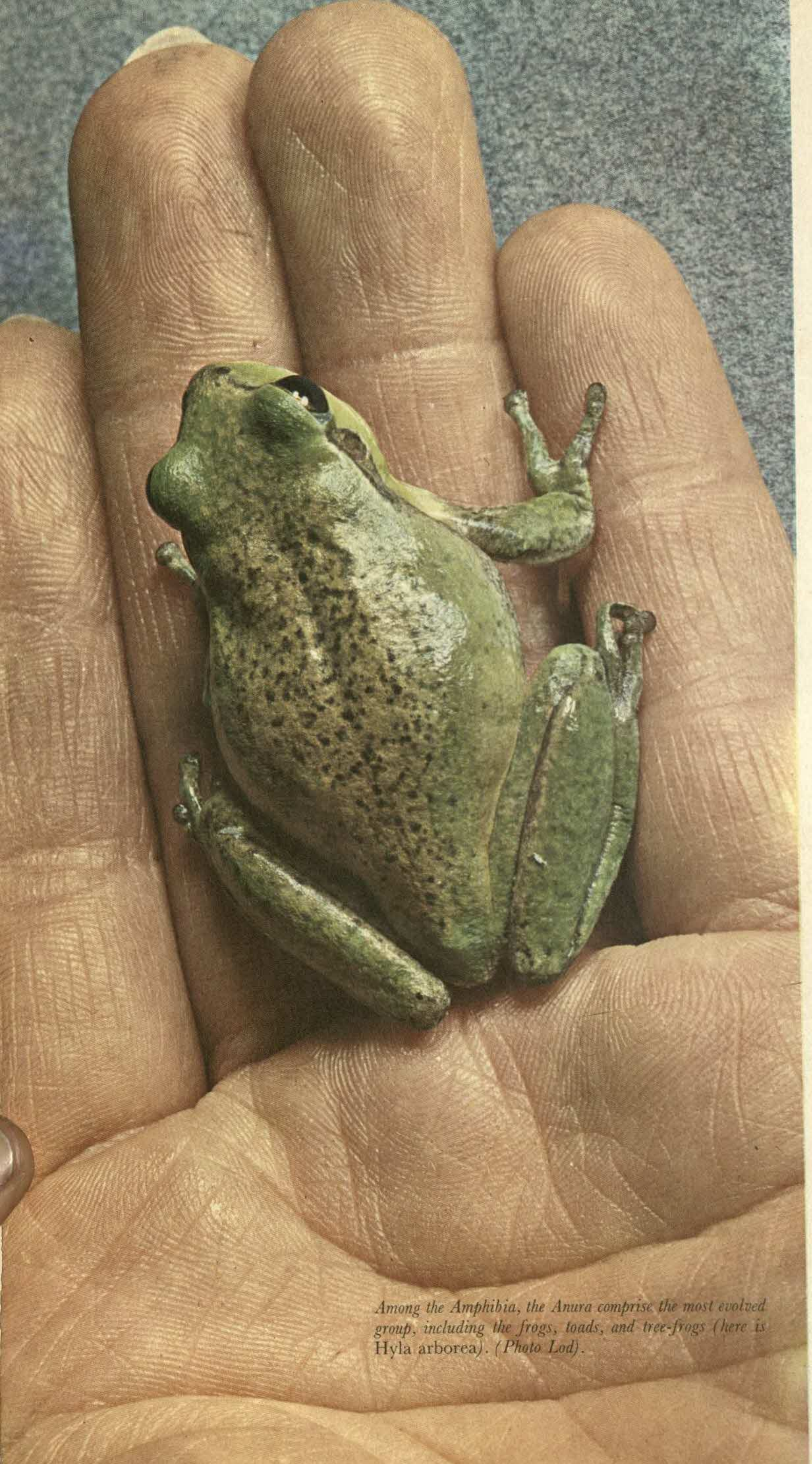
How did life upon earth begin? Nobody knows for certain; for ingenious though they are, the hypotheses put forward by biologists, chemists and astrophysicists remain theories, and until man discovers how to create life from simple elements (a possibility there is no reason to reject), we must regard their ideas with critical reserve. Today life, which is closely linked to the cellular state, exists only in relatively complex forms, of which it seems that the most primitive are the Bacteria. This assertion is in no way vitiated by the existence of viruses, for a virus cannot 'exist' until it is introduced into a cell which ensures its maintenance and synthesis.

Amongst unicellular organisms[2] it is usual to distinguish two main evolutionary streams: the plants possessing the green pigment chlorophyll, which enables them to synthesize living matter from simple mineral substances under the influence of sunlight; and the animals which, having no such ability, have to depend upon what the plants provide. Such unicellular animals are known as Protozoa.

We cannot be certain that the unicellular plants, or Protophyta, as they appear in nature today, are the ancestors of animals; for some Protozoa which feed on chemiotrophic bacteria, have apparently developed without ever passing through a stage possessing chlorophyll. So it would appear that bacteria are antecedent to cellular forms although, so far, we have no means of proving this. The need for animals to nourish themselves at the expense of plants has not limited their evolution and their forms and structures are so numerous and complex that they surpass those of plants.

The evolution of unicellular organisms has followed very different paths, but has

A young bee. It is probably in the Arthropod phylum that evolution has displayed its most lavish capacity for diversification. The insect in this picture is enlarged six times. (Photo Lod).



Among the Amphibia, the Anura comprise the most evolved group, including the frogs, toads, and tree-frogs (here is Hyla arborea*). (Photo Lod).*

never passed a certain level of complexity. Only occasionally have species of great size arisen, such as *Nummulites*, shaped like a griddle cake, which lived during the Tertiary epoch some fifty million years ago and measured about 19 cm in diameter. Even these giant forms remained as cytoplasmic masses with many nuclei, yet structurally identical throughout.

The multicellular state

There can be little doubt that the multicellular animals, or Metazoa,[3] have evolved from the Protozoa, but it is impossible to recognise amongst the protozoa of today any specific group from which they might have arisen. Neither the methods of cell-division nor the reproductive elements of the two groups are the same in these animals and the features regarded by some biologists as betraying some kind of relationship between them are more likely to be due to 'convergence'—the development of common features—than to a common origin. On the other hand, the unity of the ancestral stock of the Metazoa is attested by two very valuable facts: the uniformity of structure of the reproductive cells or gametes, and the uniformity of the reproductive cycle, during which meiosis[4] reduces each individual to the same evolutionary stage.

The multicellular state would not have been able to realize its full creative and adaptive potential without specialisation of its parts; that is, the differentiation of the constituent cells into distinct groups and the assembling of cells of one or several categories into functional systems or organs.

Evolution has continued to elaborate the organisation of animals and, by perfecting their nervous system, has endowed them with an ever-increasing command over the external environment. We know that, in some cases, events have slowed or stopped further development or even brought about a regression. But the general trend of evolution has been towards increased organic complexity and an increasingly elaborate nervous system.

As we advance up the zoological scale, we can observe the main stages through which the animal kingdom has passed.

The most primitive multicellular animals possess a simple anatomy without separate organs and with all their parts derived from two embryonic layers,[5] the ectoderm, or outer, layer, and the endoderm, or inner. This feature gives them the name of Diploblastica, and they include the sponges or Porifera (which are fixed multicellular animals, most of which live in the sea from which they draw water containing food-particles through many apertures and, having absorbed the food, eject the water through a single opening at the top), and the Coelenterata such as the freshwater hydra, jellyfish, and corals. The coelenterata are also aquatic animals, but differ from the sponges in that their two-layered wall surrounds a central cavity which has only a single opening; other familiar members of this family are sea-anemones and the floating Portuguese man-of-war.

The evolution of triploblasts

Animals with specific organs are formed from three embryonic layers, as will be explained in more detail elsewhere. In these, an intermediate layer, the mesoderm, glides in between the ectoderm and endoderm. Animals with three embryonic layers are called Triploblastica, and even the simplest possesses a complicated organisational pattern: not only do the organs differentiate but they arrange themselves in systems concerned with particular functions: circulatory, excretory, digestive, and so on. The stage of simple cavities has been passed and the nervous system is no longer a mere network of cells. It acquires controlling centres and becomes increasingly complex, giving the animal greater adaptability and new aptitudes. Whilst the ectoderm forms the skin and nervous system and the endoderm the lining of the alimentary tract, the mesoderm gives rise to muscles, the skeleton, most of the internal organs, the circulatory system and connective tissues. The simplest members of the triploblastica are the Platyhelminthes, or flatworms, of which some have a mouth and digestive tract, although these may be absent, and there is no blood system. Within this group are the freshwater flatworms and also internal parasites such as liver flukes and tapeworms. A second group within the category is the Nematodes, or round worms, found everywhere, in water, in soil, and some are parasites in the human or animal intestines.

In other members of the Triploblastica, early in development the mesoderm forms solid masses on both sides of the gut, which break up into successive blocks or somites. Each somite become hollowed out to form a cavity and cells which detach themselves from its lining go to form muscles, skeleton, connective tissue, etc.

The assembly of cavities from all the hollow somites forms what is called the coelom, the main body cavity. The coelom is more or less modified according to the phylum to which the animal belongs. In the arthropods such as crabs, insects, centipedes and spiders, and most molluscs (snails, shellfish and octopuses), the body cavity contains the blood.

The coelom, even in cases where it is obliterated in the adult, always plays an important role in the development of the individual and is a major agent in moulding the shape of the body.

Because successive somites are distributed symmetrically along the body axis, the coelom confers a segmented structure on the organism, which shows up in the repetition of pairs of organs (muscular, nervous, excretory, and genital) at the level of each pair of somite cavities. Thus the kidneys, sex glands, muscles, and nerves are the same on each side of the body. This layout becomes modified in the adult, but always leaves underlying traces.

In several phyla, the segmentation of the coelom is less strongly marked. Such is the case among the Molluscs, which are, however, related to polychaete worms,[7] the prototypes of segmented Coelomata. Among the echinoderms,[8] the segments, after complicated metamorphosis, no longer produce a linear order, but a radial symmetry, as in the starfish and sea-urchins.

The evolution of the Coelomates has taken place along a number of different routes, but two main types of structure can be recognised. In one the nervous system is ventral, with respect to the gut, in the other dorsal, that is, it is respectively in front of, or behind, the gut.

Hyponeuria[9] and Epineuria[10] constitute these two main types, and are quite distinct in form, function, and nervous system. Their resemblances are limited to the segmented condition of the mesoderm. They probably had a common origin, now lost in the distant past, as they have some embryonic similarities, but of course the evolutionary processes have been very different in each of the two groups.

The Hyponeuria include the Annelida (earthworms and leeches), the Mollusca, and the Arthropoda.[11] In the latter the nervous system has a 'brain', composed of several fused ganglia and a ventral chain composed of ganglia, at the rate of one pair for each pair of coelomic cavities. The brain and the ventral chain are united by two nerve cords situated at intervals along the gut and enclosing it like a collar.

The Mollusca,[12] which for the most part accumulate calcium from their surroundings, from which they build uni-valve shells (as in

The eel belongs to the Teleostii, *an order containing some of the most highly evolved fish, remarkable for their ability to adapt to the most diverse conditions and environments. (Photo Lod).*

---

(1) Ecology: *the science which studies species in their natural environment in order to understand their behaviour and the factors governing it.*

(2) Unicellular organisms: *primitive organisms consisting of a single cell. Those with animal characteristics are the* Protozoa, *those with plant characteristics the* Protophyta.

(3) Metazoa: *animals composed of many cells originally derived from the* Protozoa.

(4) Meiosis: *a special method of cell division ensuring that the number of chromosomes in the germ or sex cells is halved.*

The green lizard, a reptile of the Sauropsid group, one of the two great Reptilian lines of evolution derived from the Amphibia, which are themselves descended from fishes. (Photo Lod).

the snails) or bi-valve shells (as in the oyster), are without doubt related to the polychaete annelids. They both begin their embryonic development in the same way and start life with the same larval form, the trochophore. But the mollusc coelum is very weakly segmented and there is no repetition of organs along the body, which grows along a dorso-ventral axis (that is, from back to front), at right angles to the body's longitudinal axis.

It is probably among the phylum Arthropoda that evolution has displayed its greatest diversity. Millions of species have arisen from a common stock, and an infinite number more have been destroyed and their remains lie fossil in the strata of the earth's crust. Arthropods populate all the terrestrial environments: oceans, lakes, rivers, streams, plains, mountains and even glaciers. Steppes and desert are domains to which they adapt themselves very easily.

The body segments, which resemble each other more closely in the young embryo, join together in places to form regions for specialised functions. In the cases of the Crustacea and Insecta they form the head, thorax and abdomen as is readily observable in the bees and wasps. The appendages are specialised according to the region to which they belong and tend to decrease in number and disappear on certain segments. This reduction is most marked among the insects, which, in addition to the head, have only three pairs of legs attached to the thorax.

The chief classes of the Arthropoda are:

1. The Crustacea, mostly creatures living in fresh or salt-water, such as crabs, shrimps, water-fleas, and the sedentary barnacles, all of which have two pairs of antennae.

2. The Myriapoda. These are the millipedes and centipedes, which have only one pair of antennae and numerous pairs of legs.

3. The Insecta. This is the largest of all animal groups with more than 850,000 species. The body has a head with one pair of antennae or feelers, a thorax or 'chest' of three segments, each bearing a pair of legs, and an abdomen. Usually the adult form possesses wings. Flies, bees, wasps, ants, butterflies, moths, beetles, dragon-flies, cockroaches, locusts, grasshoppers, lice, and earwigs all belong to this enormous group.

4. The Arachnida. These are mostly land-living animals breathing air, with no antennae and four pairs of legs, such as the scorpions, spiders, and mites.

The crustaceans, myriopods, and insects are sometimes classified together in the larger category of Mandibulata, the Arachnida in the category of Chelicerata, and there is a third category, the Trilobita or trilobites, marine arthropods which flourished in Paleozoic times about 600 million years ago.

From these three major categories of arthropoda spring many secondary lines.

The Echinodermata are the most acephalous animals (that is, they show no sign of a head). In the adult state, most of them are constructed on a pentaradial symmetry with five branches radiating from a common axis, and there is a chalky skeleton just beneath the surface. Included here are the sea-cucumbers, starfish, and sea urchins, and the stalked sedentary sea-lilies which inhabit the ocean depths. This is a group with a long geological history and many extinct forms are known.

The Hemichordata live either isolated and buried in the sand, or in large colonies in their tubes, and are characterised by a pharynx communicating with the exterior by pores or branchial slits, and a structure resembling the notochord of Chordata; whilst the Pogonophora, discovered a few years ago, live on the bottom of the sea and resemble very fine worms. They have no gut.

The evolution of vertebrates

The epineurian coelomates are known as Chordata, a term used of all animals which have at some period of their life an organ which functions as a supporting rod, the notochord. In some of the lowliest members of this group this elastic rod is present only in the early stages of their life, whilst in the highest it is finally replaced by the spinal column or backbone. Other features shared by the chordata are the presence of gill-slits either throughout life or during some part of it, and a central

(5) Embryonic layers: *layers resulting from the folding inwards, like the turning inside-out of the finger of a glove, of the original blastula or hollow ball of cells formed during the early stages of development. The outer layer becomes the ectoderm, the inner layer the endoderm and, in the higher animals, the mesoderm comes in between.*

(6) Parenchyma: *the connective tissues of the embryo and lower* Triploblastica.

(7) Polychaete worms: *a primitive group of worms, free-living, segmented, provided with locomotory bristles, and bisexual.*

(8) Echinodermata: *marine animals, such as the sea-urchin, which are radically symmetrical and usually possess a chalky skeleton under the surface which sometimes bristles with spines.*

(9) Hyponeuria: *those species in which the nervous system is below the gut.*

(10) Epineuria: *those species in which the nervous system is above the gut.*

nervous system. There is no general agreement among zoologists about the creatures which may be included in the chordata; for, although three phyla of very unequal significance are generally included, the Tunicata, the Cephalochordata, and the Vertebrata, opinions vary as to the claims of the Tunicata. The Tunicata are marine animals consisting of about 700 species, some leading a pelagic life (i.e., moving freely between the surface and the sea-floor) and living on plankton, whilst others remain fixed to the rocks of the sea-floor. They are usually classified as protochordate animals, coming between the true chordata and simpler forms of life. At some time in their life gill-slits are developed, and the larval forms usually have a tail supported by a notochord, as in the sea-squirt.

The Cephalochordata of which *Amphioxus*, the common lancelet, is a classic example, demonstrate the structural plan of the Chordata to perfection, although their excretory apparatus, composed of protonephridia,[13] is of a peculiar type, characteristic of many invertebrates. *Amphioxus* is not the direct ancestor of the vertebrates, but, arrested in its evolution by its very specialised mode of life (its body is planted vertically in the sand of the sea, where it feeds on microscopic creatures), it has kept the essential chordata traits.

The Vertebrata have had an extraordinary history. They are distinguished from *Amphioxus* by their brain and vertebral column which, composed of bone or cartilage, replaces the notochord. In the embryo, at least, three regions are distinguishable: the head, containing the brain where messages are received and actions largely initiated, the trunk, containing the internal organs, and the propulsive tail (originally used for swimming).

The evolution of the vertebrates is directly associated with the development of the nervous system, which goes with the increasing importance of the head. Various tissues are brought together to form a capsule, the skull, which is at first cartilaginous and then becomes bony.

The evolution of the lowest types of vertebrate, the Cyclostomes and Pisces, took place, of course, in an aquatic environment. The cyclostomes, although usually grouped with the fishes, are separated from them by various characteristic features: they are eel-like with a gristly skeleton, persistent notochord, scaleless skin, and a jawless suctorial

Three-coloured Barbet: remarkable morphological specialisation is found among the birds. (Photo Lod).

mouth which they use to attach themselves to their prey, from which the flesh is rasped off by a toothed muscular tongue. The most familiar members of this group are the fresh-water lamprey and the common hag-fish. The passage of life from water to the land was only made possible when the gills came to coexist with an aerial respiratory organ, originally derived from the swimbladder. The present-day Dipnoi, or mud-fishes, possess this double-breathing apparatus with gills as well as a lung-like swimbladder. Later in evolution the gills disappeared and only the lungs persisted.

The development of the brain was speeded up by the conquest, first of the land, and then of the air. The gill-slits persisted only in the embryo and the tail region tended to lose its importance. Paired fins were replaced by limbs, whose structural plan has hardly changed from amphibian to man. All the vertebrates from the amphibians upwards are tetrapods or four-limbed. The framework of the gills loses its respiratory function, is partially lost, and plays an increasing part in the formation of the skull which also annexes the front vertebrae or segments of the backbone, whilst the first spinal nerves are incorporated in the hind-brain in the occipital region at the back of the head. The primitive kidneys are replaced by new organs, the metanephros.[14]

Guinea-pigs are familiar little mammals derived from a wild stock from the high Andes plateau. They are now used as laboratory animals, because of the ease with which they may be reared and experimented on.

The brain has undergone a double evolution. It has increased in volume, largely owing to a rise in the number of neurones or nerve-cells, and it has diversified its parts, increasing the number of types of neurones.

The Amphibia, which arose from the fishes, include frogs, newts, toads, and salamanders, equally at home on land or in the water. These gave rise to two great evolutionary lines: the Sauropsida and the Therapsida. The first includes the sauropsid reptiles and the birds, the second the therapsid reptiles and mammals. The former comprises the modern reptiles and others in which the limbs came to be highly adapted for flight, as in the extinct pterodactyls, the latter were mammal-like reptiles living two or three hundred million years ago which radiated into several varied groups and gave rise to the mammals.

Following extensive modifications, the lower jaw passed in part to the service of the middle ear. The development of the brain proceeded parallel in the two lines, but in the Therapsida, not only were the transformations more rapid, but they were more varied, permitting the animals to lead less specialised and narrow existences. In the two lines Therapsida and Sauropsida, increasing independence of environment finds expression in the maintenance of constant control of the internal environment (temperature, composition of body fluids) by means of regulatory systems involving the co-operation of the nervous system and endocrine glands. Thus the cold-blooded reptiles and amphibia are wholly dependent on the temperature of their environment, whilst the warm-blooded birds and mammals regulate themselves to many different environments.

The birds have gained in morphological and physical specialisation, although their brains have remained at a fairly low level of development and their behaviour has not freed itself from automatism.

The mammals, on the other hand, very soon showed a tendency to diversity which enabled them to penetrate the most varied environments, some of them, like the whales, even returning to an aquatic environment without losing their lungs. The evolutionary potential of the mammals has been due to the preservation of many stocks of a 'generalised' structure not marked by rigid specialisation.

It is thus that the Insectivora have given rise to the primates, some of which have developed their brains freely, leading to the origin of man.

(11) Arthropoda: *jointed organisms segmented like worms. The joints are rendered necessary by the presence of chitin, a tough material on the surface of the skin. Their jointed appendages are adapted to many very diverse functions and the body cavity is reduced to a collection of spaces within which the blood circulates. The nervous system consists of a chain of ganglia with a simple 'brain'. Development is interrupted by a series of moults and very often accompanied by metamorphoses, as in the transition from chrysalis to caterpillar and the final form in butterflies.*

(12) Mollusca: *animals with an unsegmented body composed of a head, a visceral mass and a foot. The visceral mass is hidden entirely or partially by a mantle which secretes a shell. The nervous system consists of a double ring around the oesophagus or feeding-tube. The body cavity is reduced to pericardium, genital and excretory organs.*

(13) Protonephridia: *a very primitive excretory organ, present in many worms.*

(14) Metanephros: *the final stage of the embryonic kidney.*

PART ONE

4008

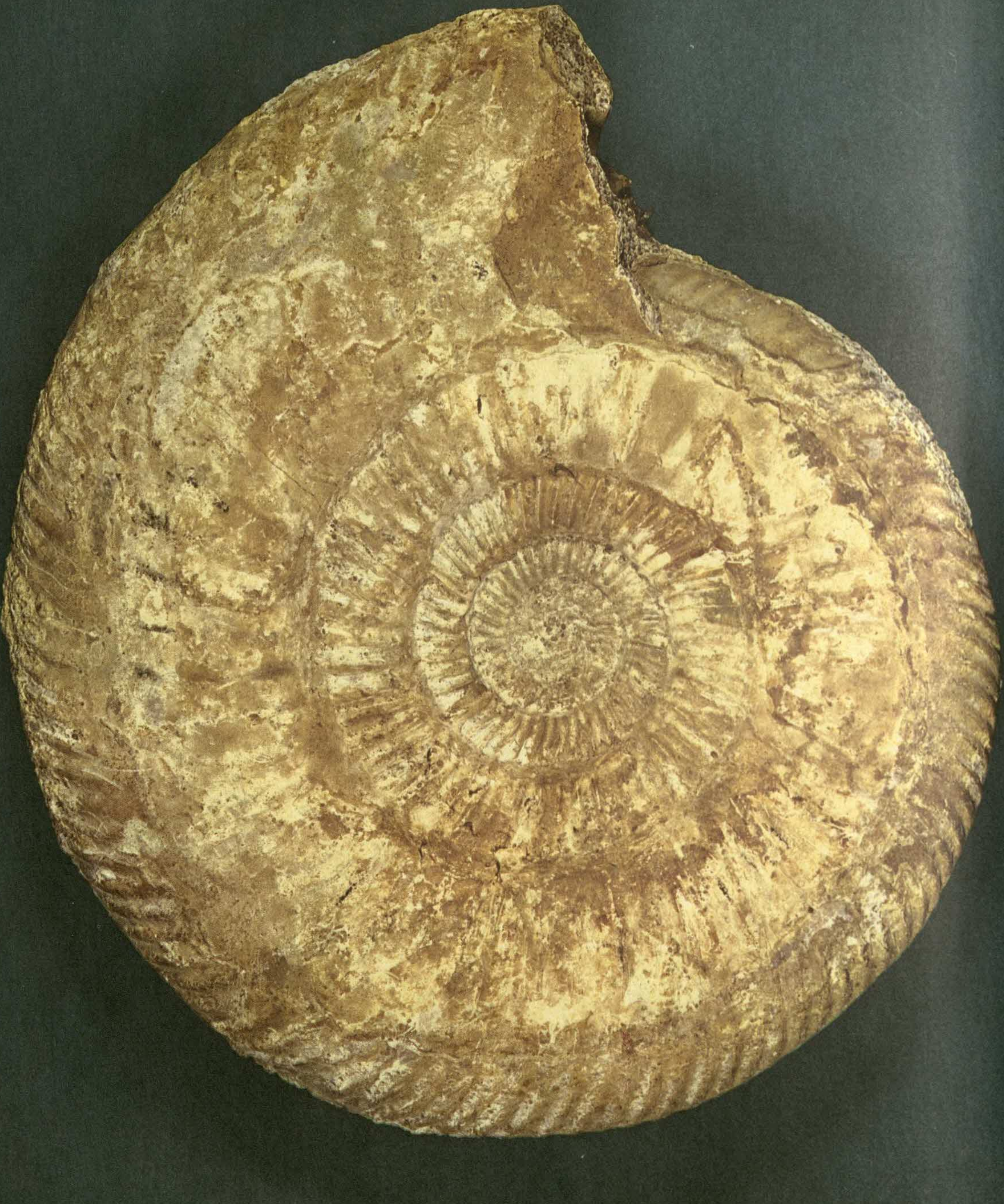
S.C.E.R.T., West Bengal
Date 7-5-87
Acc. No. 4006

S.C.E.R.T., West Bengal
Library
Calcutta
25/3, B. C. Road

State Institute of Education
Banipur

Animals and time

Oysters, living and fossilised. (Photo Lod).



Outlines of palaeontology

André de CAYEUX

The main evidence about life as it existed in the distant past comes from the study of fossils. The imprint of a fish on a piece of shale tells us what kind of animals inhabited the seas three hundred million years ago. Our museums are full of such relics; shells, bones, footmarks and imprints of all kinds, which are the subject of study of palaeontologists. Altogether several hundred thousand different species of fossil are known.

In spite of all this apparent profusion of specimens, the palaeontologist lacks complete information. Whole groups of the animal kingdom which are soft and have no shell or skeleton, such as jelly fish, annelid worms, and many single-celled organisms, have disappeared almost without trace. For every fish which has left its imprint on the rocks, countless more have gone forever. This is even more true of land-living animals, which run a great risk of being eaten, or rotting away, rather than being buried in the mud of a lake or sea—the conditions in which most fossils are formed. As an example, our knowledge of the evolution of birds rests on three fossil specimens of *Archaeopteryx* which was, presumably, a fairly common animal.

With such fragmentary information to rely on palaeontologists are naturally cautious. But today they are increasingly applying those statistical methods which have been proved so useful in other fields. When a Gallup poll measures public opinion, a poll is taken which involves only a small fraction of the total population, perhaps one in a thousand or one in ten thousand, and provided the sample that is chosen is representative, the opinion of the sample is a good estimate of the opinion of the public as a whole. In just the same way, fossils can be regarded as a sample of all the animals which have lived in the past. We are therefore justified in letting them speak for the past, provided we are satisfied of the extent to which they are a representative sample of the whole.

The apparent explosion of life in the Cambrian period

The age of a fossil can be estimated from the age of the rock in which it is discovered. Over the years layer upon layer of sedimentary rock has been built up as silts or other material were deposited in seas or lakes. Thus the older the fossil the deeper the layer of rock in which it is found. Until quite recently this dating was only comparative, but for the past few decades we have been able to obtain an estimate of the true age, from the proportion of certain radioactive isotopes, notably those of lead, that they contain. Thus we know that about six hundred million years have elapsed since the beginning of the Cambrian period (called after Wales, where the shales and limestones of this era impose their dark colours on the landscape), and at least three thousand million years had passed before this epoch started. It is only from the inception of the Cambrian that we begin to find fossils in relative abundance in the rocks. In the pre-Cambrian rocks they are exceedingly rare and the known deposits of these are so few that they could be counted on the fingers of both hands. In each one the species found are rare, consisting of little more than a few unicellular organisms or the occasional imprint of a worm or crustacean. The oldest known deposit, in Canada, dates from about 2,600 million years ago and embedded in it an alga, a filamentous fungus, of an estimated age of 1,700 million years has been discovered by E. S. Barghoorn. The scarcity of fossils is all the more surprising when contrasted with the very considerable variety in the following period. In the Cambrian rocks all the main classes of present-day animals are represented, with the exception of the vertebrates, and some of these creatures have very complicated forms, such as the trilobites, which are related to our crustacea. From what we know about the speed with which various forms succeed one another, it seems certain

HISTORICAL NOTES

15,000 years ago

Our prehistoric grandmothers bored holes in fossil shells to make necklaces and pendants. At Brno in Moravia, a necklace has been found made of 600 such shells.

In the fifth century B.C.

Greek and Egyptian thinkers described 'shells which were to be found in the mountains'. From this, according to Herodotus, they quite rightly deduced that the sea formerly covered what is now dry land.

13th century

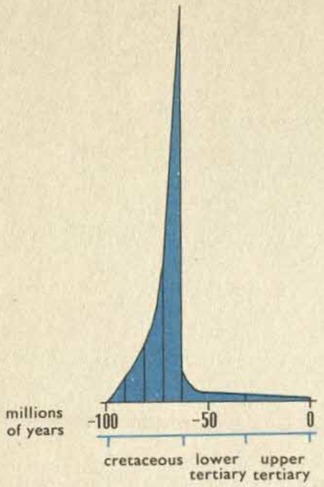
ALBERTUS MAGNUS, *the scholastic philosopher, once more put forward the correct interpretation of fossil imprints found at Paris, as the Greeks had earlier. His views were ignored.*

1580

BERNARD PALISSY, *a French potter and enameller, who also lectured on natural history in Paris, held the same views; for the first time he distinguished between marine and freshwater fossils.*

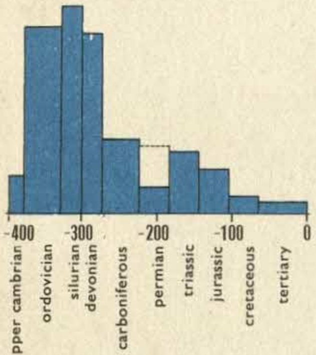
(Continued on page 30)

During the secondary, or Mesozoic, epoch life spread over the surface of the globe and certain groups, like the ammonites (see opposite page), produced a great luxuriance of evolutionary forms. (Photo Lod, Gallery of Palaeontology, Muséum, Paris).

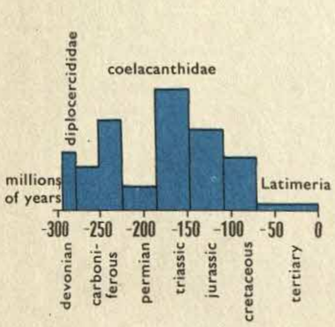


Variations in the number of species of Salenia *from the Cretaceous to the present time. (Coloured area proportional to numbers).*

Variations in the number of species of Lingula *from the upper Cambrian to the present.*



These graphs are based on calculations made some years ago by A. T. Holmes. His more recent research shows that the times for the various groups should be increased by about 20 per cent, as will be apparent from figures in the text.



Number of species of coelacanths at various periods. They appear in the carboniferous and reach their climax of development during the Mesozoic era.

that the animals of the Cambrian period must have had a very long history and a lengthy series of developmental stages up to this point. Yet geologists have found no trace of these earlier steps in the evolutionary process. Why are pre-Cambrian fossils so extremely rare?

Perhaps the sudden explosion of life in the Cambrian is not an illusion and may actually have happened; for just before the Cambrian there was a long glacial epoch and experience based on the more recent ice ages suggests that this would have presented a major crisis for most living things. It is not simply the cold weather which is a hazard but the increased salinity of the seas, resulting from the fact that a large part of the earth's fresh water becomes locked up in the vast areas of ice. After such a crisis a period of expansion occurs and new species arise to fill the gaps left by the elimination of the old forms, just as the human population tends to increase following a major war. Possibly a similar expansion began in the Cambrian after a particularly severe crisis.

But this still does not explain the astonishing complexity of the trilobites and other animals which suggests that they must have had at least a few similar predecessors. Where are the traces of these? In nine cases out of ten, or even more often, it is likely that they were simply wiped out. This is because the pre-Cambrian rocks, which originated in slaty or chalky muds, or in sand, have since been transformed, buried and heated, recrystallised, reheated, and have gone through many other changes. In the crystalline masses any fossil traces that may have been present become unrecognisable. We know that this has occurred and it certainly accounts for a good deal.

But it does not explain everything. In the western United States, in the Grand Canyon of Colorado, and the Ahaggar mountains of the Sahara, some pre-Cambrian rocks escaped this reheating process and there are shales, sandstones and chalks which are clearly recognisable as being almost identical with those of the Cambrian. Yet they contain no fossils, except for the extraordinary fossils of the alga *Collenia.* We know that in Cambrian times life was confined to water, presumably to the sea, and it seems likely that the same was true earlier. From this it might be deduced that if these well-preserved rocks were laid down on land, or in fresh water, the lack of fossils would be understandable.

Are these tenable explanations? Confronted with the fascinating problem of the origin of life on our earth, the palaeontologist must confess he has insufficient direct evidence. It is to the bacteriologist or the physiologist that we must turn to help us to visualise how life began. One view is that biological evolution was preceded by chemical evolution which led eventually to the development of large organic molecules reproducing themselves much as the viruses do today. From these 'living molecules' the first simple organisms evolved and they led to the many animals and plants which we now know.

Evolution, or separate creation?

This immediately raises a question. Are all the different species derived from one another, as the theory of evolution suggests? Or have they appeared independently as unrelated types, as the French naturalist, Cuvier, maintained a hundred and fifty years ago? At present at least 99% of all biologists accept the theory of evolution, and we shall use its terms here. But it is a curious fact that all the implications of evolutionary theory would be equally true if there had been no evolution but simply a succession of creative acts without causal connection, so everyone can choose the hypothesis he prefers.

If we compare the enormous number of species of fossilised animals since the Cambrian with the length of time that they have existed, we are immediately struck by the inequalities. Take, for example, the genera or groups of animals which resemble each other, like the dog, the fox, and the wolf. Amongst those existing today some, like horses, cattle, and elephants are recent, since they have existed for no more than a million years. But moles, hedgehogs, hares, and rats go back 20 million years; bats and squirrels, 40 million years; and the sea-urchin *Salenia* goes back 120 million years.

Nor is that the limit. Oysters existed 180 million years ago, as did the shellfish, which the naturalists call *Pinna*, and the small sea-urchin *Nucleolites*, which is hardly bigger than a hazel nut. A little earlier lived the important genus *Apus*, a broad-backed crustacean which is indistinguishable from the species which still swims in fresh water today. *Apus*, in fact, takes the record for the same species back to no less than 200 million years ago.

If we look at the next largest category, the genus, we can go even further back. Almost 250 million years ago we find the *Trigonia*, a triangular shellfish which lives nowadays around the coasts of Australia, and also a Limulus very much like that which now lives in

The imprints of some fish have been preserved with extraordinary precision. (Photo Lod).

North America and in the East Indies. The tuatara reptiles originated about the same time, and their last survivors now haunt the rocks of an island off the shores of New Zealand where they nest in the same burrows as the petrels and live off the crumbs left from their feasts.

Still 250 million years ago we find the large-spined sea-urchin *Cidaris*, and from the period of the Carboniferous forests of 315 million years ago we have a spider scarcely different from our wolf-spiders and a small snail *Pupa*, which, as the name suggests, closely resembles a butterfly pupa, as well as a keyhole limpet just like that found on beaches today. 420 million years ago there were already small bottle-shaped shells, *Lagena*, and the wheel-shaped *Rotalia* among the foraminifera. There were also the bivalves, *Nucula* and *Leda*, like those of our coasts, and a papery *Nautilus* similar to that which still drifts in the sea around Indonesia. As far back as 500 million years ago an ancestor of *Peripatus*, half worm and half arthropod, was miraculously fossilised together with *Lingula*, the oldest of the genera which was recognisable then, as now, by its thin shell made up of two similar and almost rectangular, valves. The cockroaches, including our common black beetles, are another very ancient family, whose ancestry goes back 300 million years to the Carboniferous period, as do the Collembola, the very first insects, wingless then as now. The collembola of today live in the soil, yet their ancestors of 300 million years ago were already paddling in the marshes of Scotland.

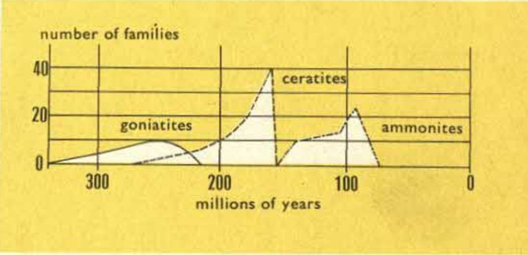
Panchronic animals

The name 'panchronic', which means 'living at all periods', is used to describe these persistent forms and in many cases they have been found as fossils before the discovery of the corresponding living species. Thus the *Pleurotoma*, shellfish with spiral cone-shaped shells, were described in 1842 in rocks in Normandy dating from 170 million years ago and two years later living forms were found in dredgings from the seas around Japan. The horny plaque-like teeth of the fish *Ceratodus* had been found in European deposits dating from 220 million years ago some time before the fish was rediscovered in Australia.

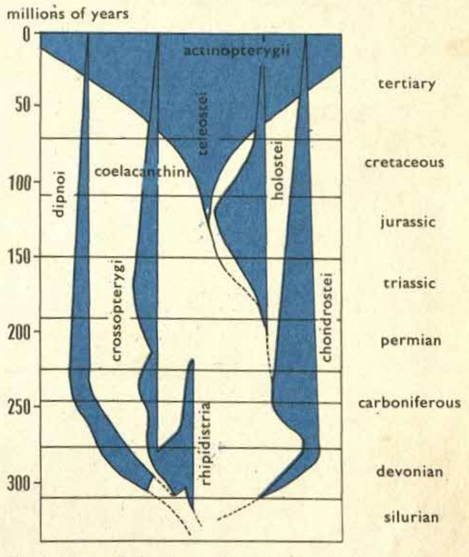
Among the oldest molluscs which originated 500 million years ago, are certain archaic forms which were believed to have become extinct 370 million years ago. But that was before a living specimen was dredged up from 13,000 ft, off the west coast of Mexico in the Pacific by the Danish oceanographic ship *Galathea* and recognized by H. Lemche. This modern genus, *Neopilina*, differs somewhat from its fossil predecessors but is clearly of the same family as is demonstrated by its muscles and gills which are arranged in regular pairs showing its distant relationship to the annelid worms. The Coelacanths were known as fossil fish dating from 370 million years ago with fins attached in such a way as to indicate a transition towards air-breathing vertebrates. They were believed to have been extinct for 100 million years until several living examples were caught, first off South Africa, then off the Comoro islands near Madagascar, and studied so successfully by J. Millot. They were found to have a lung, a simple skeleton without vertebrae, a very small brain (only 1/15,000 the weight of the body), and an elongated heart which was much more primitive than that of any present-day vertebrate.

The coelacanth is a living fossil. For more than 350 million years, other species have appeared and disappeared around it, and the face of the earth has changed many times but the coelacanth itself has remained almost unaltered. How has it managed to survive and adapt itself to all these upheavals?

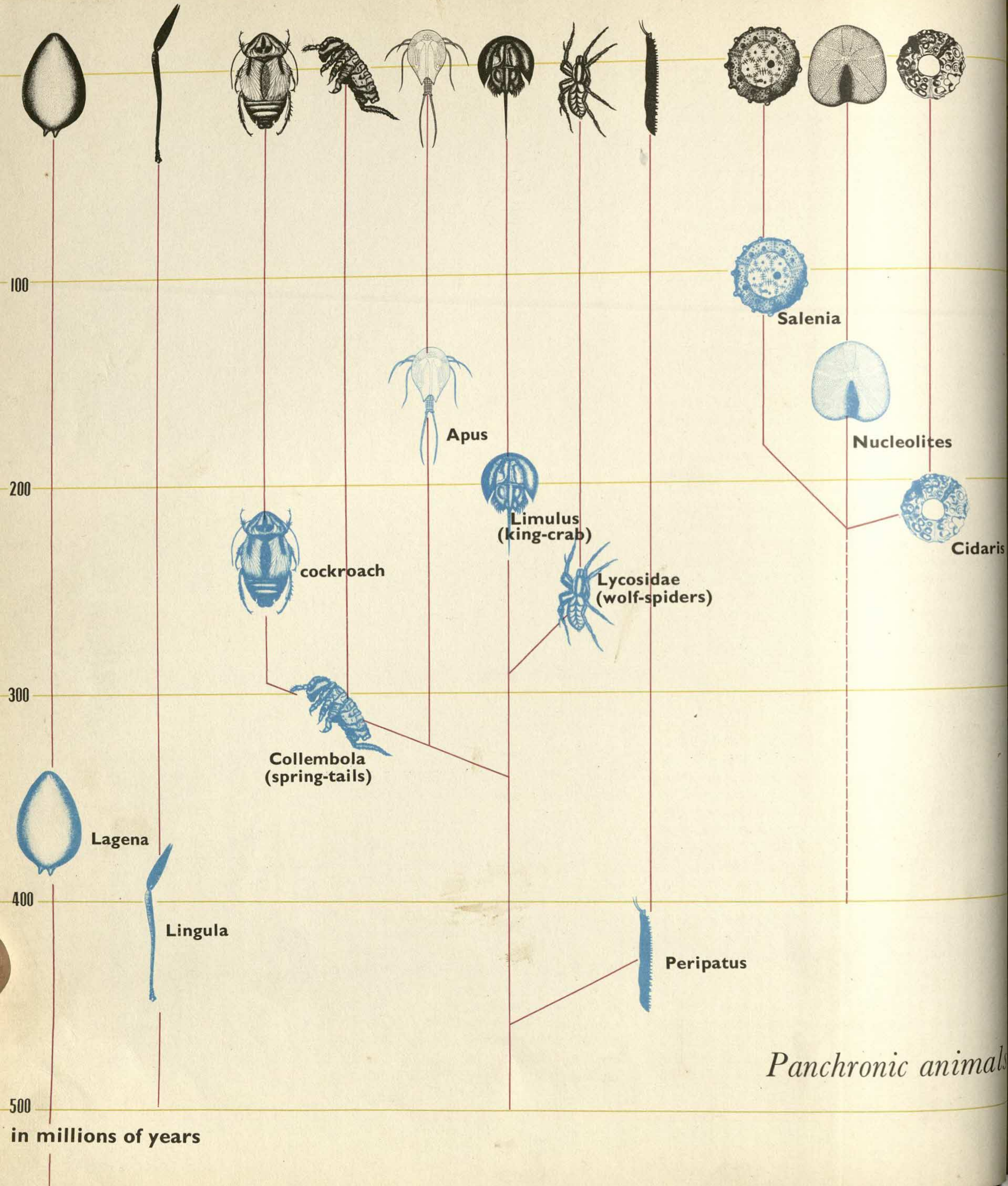
In deciding this we must recognise the limits of this case and others like it. Panchronic organisms have changed very little but they have nevertheless changed. The first lingulas were smaller and narrower than ours and the lung of the present-day coelacanth is quite useless since it is infiltrated with fat. Panchronic animals often belong to rather specialised



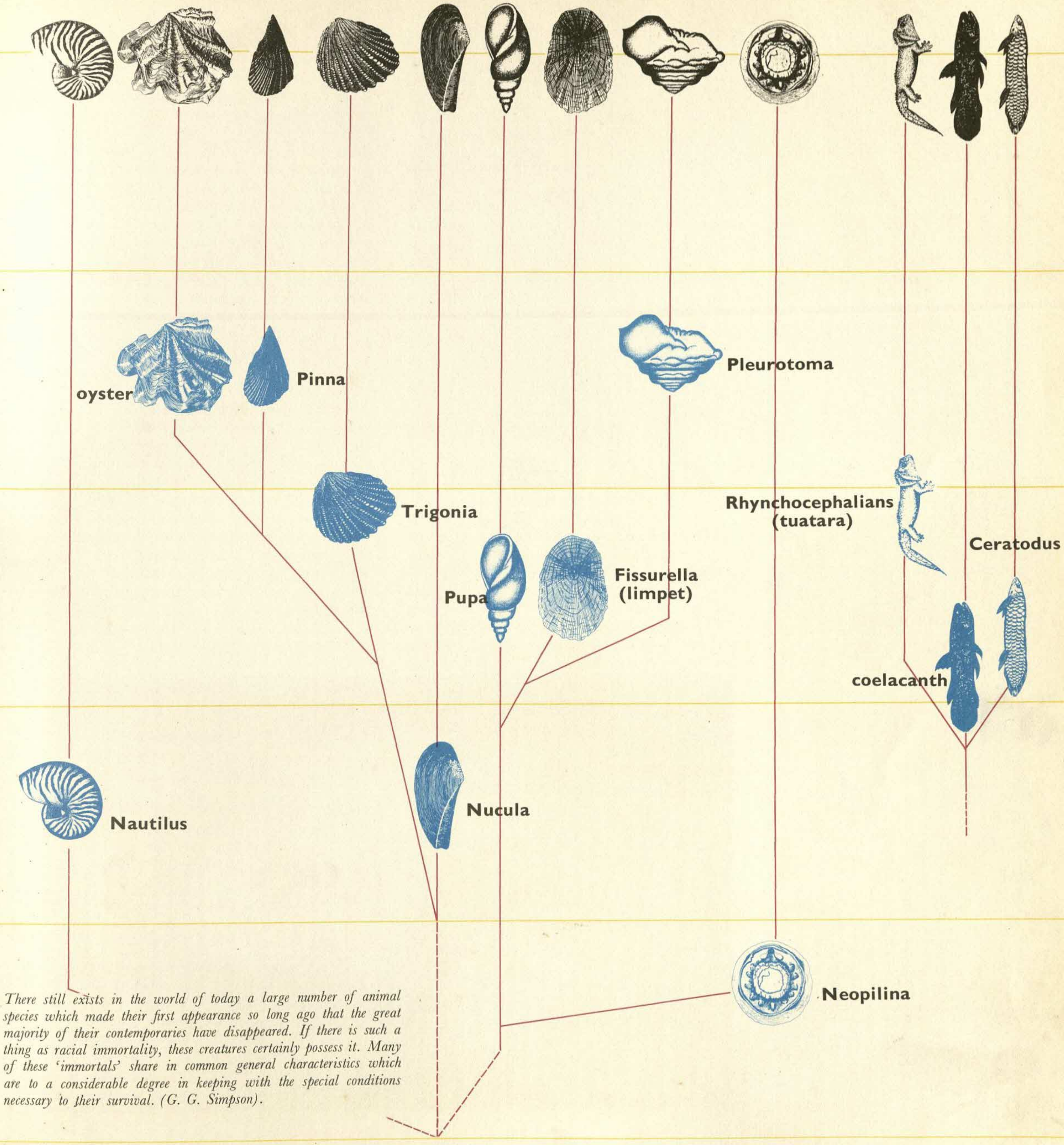
The succession of groups of ammonites in the course of time.



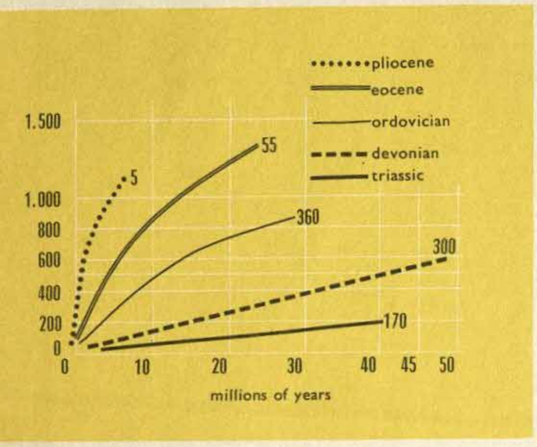
Evolution of the bony fish during geological times. (After A. S. Romer).



Panchronic animals



There still exists in the world of today a large number of animal species which made their first appearance so long ago that the great majority of their contemporaries have disappeared. If there is such a thing as racial immortality, these creatures certainly possess it. Many of these 'immortals' share in common general characteristics which are to a considerable degree in keeping with the special conditions necessary to their survival. (G. G. Simpson).



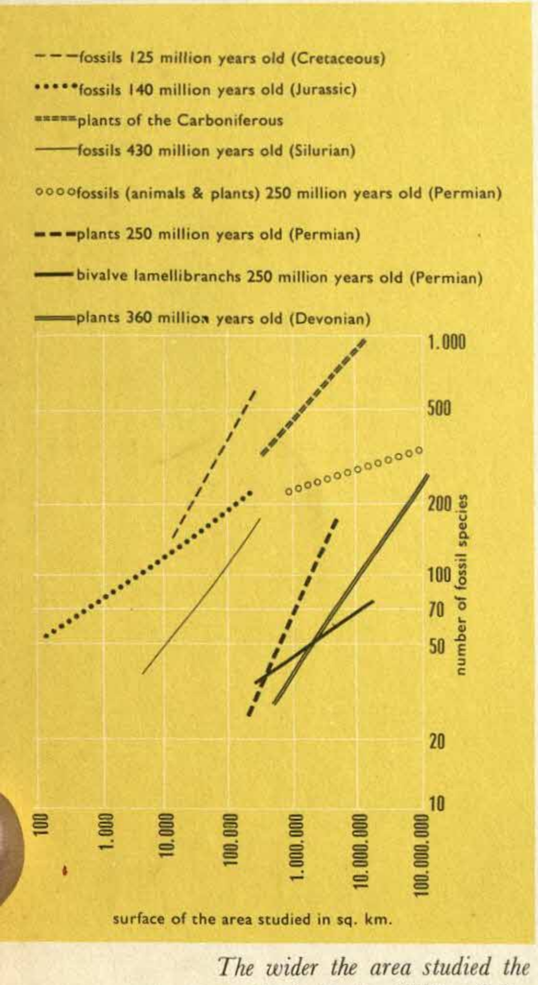
In the course of time the total number of species has grown in geometrical progression.

groups with few species and genera, as in the case of nautilus and limulus. In the world of today they play a very small role, being mere relics confined to obscure refuges, such as distant islands or extreme depths.

Finally, the fact that they have existed for so long makes them the rarest of exceptions. More than half the fossil genera lasted no more than twenty million years and half the species less than six million. But, as in all statistical distributions, there are variations around the mean. Some forms last for a short time, others for much longer, and it is these latter that we call panchronic. The majority of them belong to groups with multiple affinities and it is perhaps due to their biologically mixed nature that they have succeeded in surviving so long in spite of the hazards of competition. For instance, the African cousin of *Ceratodus* lives equally well in dried mud or in water; *Neopilina* has been able to adapt itself to very deep water, and the ancestors of the tuatara quite certainly did not frequent the nests of petrels, since at that time birds did not exist.

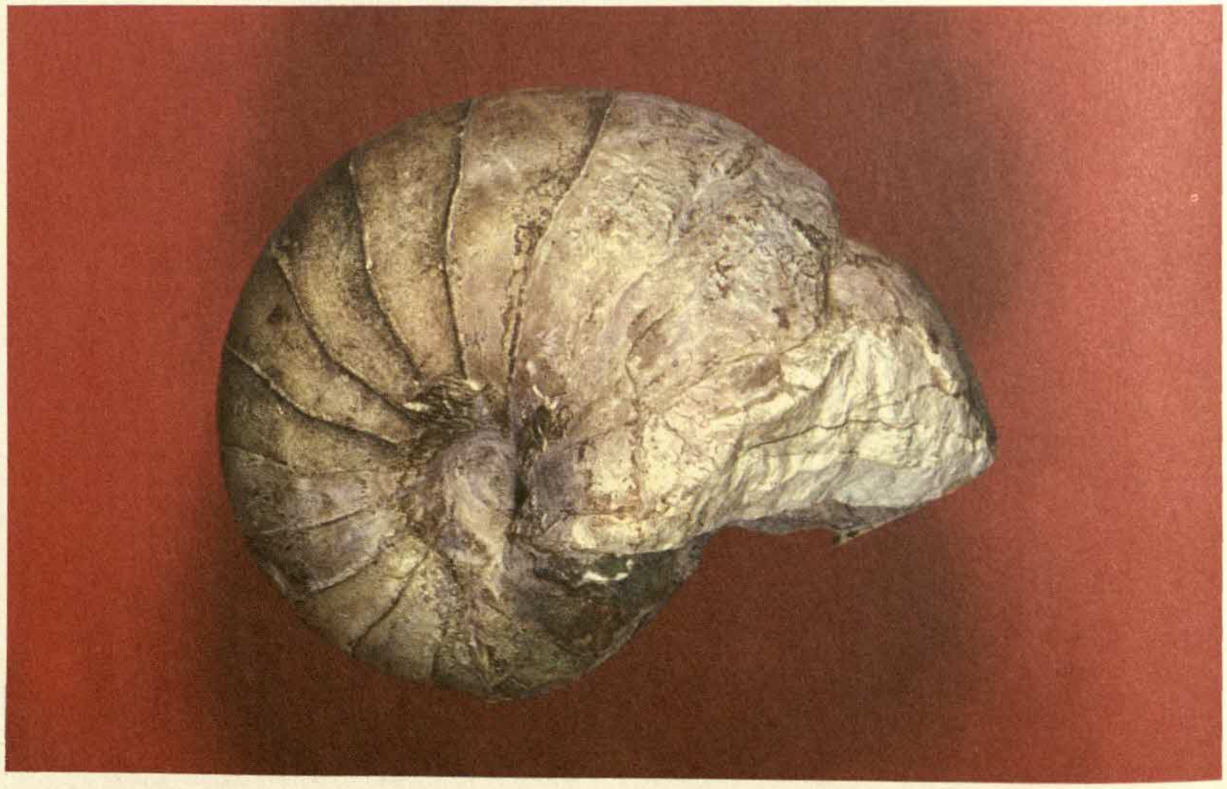
The use of the statistical approach, which has increased our understanding of the panchronic animals, also throws a new light on other aspects of life in the past. Let us first take a simple group, a genus for example, which is made up of various species. Initially, the number of these which are coexistent increases with the passage of time, often in geometric progression—a fact which was demonstrated for the first time in the case of diatoms by Professor J. Small, of Belfast. The genus then passes into a phase when the number becomes stationary, and then declines. The pattern is the same for genera of the same family, and for families of the same order. As time passes, groups succeed each other. Among the marine molluscs with large tentacles the Goniatites appeared and then died out. Their place was taken by the Ceratites, which disappeared in their turn, to be replaced by the Ammonites whose rolled-up shapes suggest the horn of Jupiter Ammon.

In the past history of animals and plants these successions are the rule. We may therefore ask if these events all took place at the same time for different series with different modes of life. Have there been a series of cataclysmic events which are responsible for these changes? The answer given by geology is ambiguous, because, although such events occurred, they did not always coincide. The great changes and renewals among the land plants took place 125 million years ago, that is sixty million years before those among the mammals. *Nummulites*, the small coin-shaped creatures, which for long ages swarmed in the



The wider the area studied the greater is the possibility of discovering fossils of different species which flourished at the same epoch.

This photograph shows a fossil Nautilus, one of the best known of the panchronic animals. The ancestors of the present-day nautilus lived 350 million years ago. (Photo Lod, Gallery of Palaeontology, Muséum, Paris).



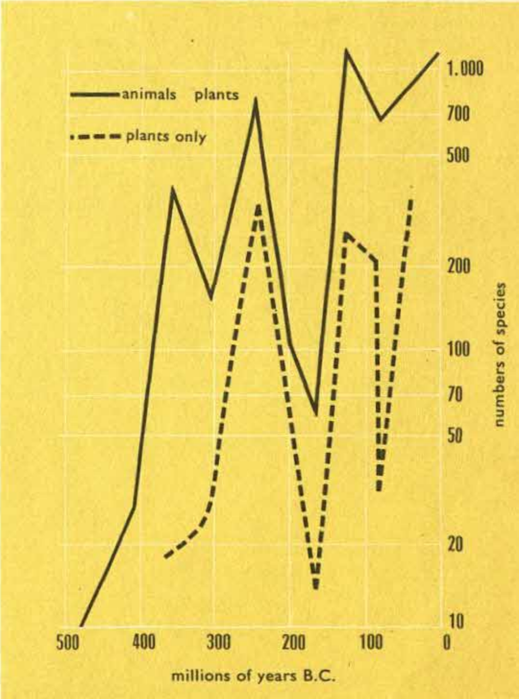
A fossilised eel, fifty million years old from the deposits of Monte Bolca, Italy. On the stone, which has been split with great care, can be seen the impression and counter-impression of the animal which was imprisoned there. The impressions are remarkably clear. (This photograph, like that of the Nautilus, has been reproduced through the kindness of Professor Lehmann, of the Gallery of Palaeontology, Musée de Paris. (Photo Lod).

sea, suddenly disappeared twenty-five million years ago, whereas other groups passed through this epoch without any trouble.

At other times, however, events did coincide and it is often easy to see why. The foraging insects began to thrive vigorously sixty million years ago at the same time as the beautiful coloured flowers which they live on and pollinate. Since these two groups cannot live without one another, it is logical to suppose that their mutual adaptation must have occurred at the same time. More wide-spread changes affecting all forms of life and probably caused by some external factor become apparent if we consider the statistics of all the fossil species in a given area. The most severe of these crises (during which the number of species was cut to 1/15 of its original figure) occurred at the end of the Palaeozoic era, about 230 million years ago, coinciding or very nearly coinciding, with a period of intense glaciation. Afterwards the number of species increased very rapidly. Life continued but mainly through the emergence of new forms.

This brings us to one of the crucial questions of palaeontology: has past life consisted of a series of cycles, with all crises leading back to the starting-point with only the participants changing? Or has there been more or less steady progress in a clear-cut direction? One has to be wary of appearances and subjective impressions; for when we consider the various pieces of evidence about life in ancient times, it is only too easy to pick out those which show cycles, or, alternatively, those which do not. It is safer to count up known cases, choosing carefully compiled lists which are as complete as possible. One of the best of these has been drawn up in Britain and from this the change in the number of species in the course of time becomes quite clear. The overall effect appears as a steady doubling of the number of species approximately every 80 to 100 million years.

One could of course object that, if the ancient species are less numerous, it is because they had less chance to become fossilised. Or that erosion has destroyed the fossils. There is the added factor that the older the deposits the more likely they are to be metamorphosed, destroying the fossil record. But if we take the same type of deposit such as sandy sea-shores containing shellfish of the period, and for each period the deposit that is richest in species, a general study shows that the chances of fossilisation are identical from one epoch to another. We find that in these shellfish from the Cambrian to the present-day there exists the same geometric progression, with a doubling of the number of species every 80 to 100 million years. The same form of progression occurs in all the large groups which have been studied, and of the six such studies so far, the only difference between the pictures obtained has been a different value for the doubling time. This law is the simplest that could be imagined: growth at a constant rate. Naturally we are tempted to apply this retrospectively too, into the pre-Cambrian times. For animals of the muddy sea bottom this suggests that there was just one single species some 2,000 million years ago.



The number of species as a function of the length of the epochs. The longer the span of time, the larger the number of different species found.

Growth in number, size, and complexity

To return to the more secure ground of the periods represented by fossils from the Cambrian up to the present-day, animals, like plants, have increased in numbers, but also in size, complexity and diversity. The change in size has long been recognised as it is extremely obvious. Thus the pre-Cambrian invertebrates had a maximum size of 1½ inches (lingula). The size increased to 6 inches in the Cambrian (jellyfish) and to 6 feet for a shellfish with tentacles of 420 million years ago, while the huge squids of today may attain

HISTORICAL NOTES

(Continued from page 23)

1678
LISTER *believed like many others that fossils were sports of nature, but, he added, 'they are animals which have disappeared'. This was a correct hypothesis, but at that time a bold one. With the exception of Robert Hooke, nobody paid any attention to him.*

1779–1784
GIRAUD-SOULAVIE *observed of the fossils of the Vivarais that 'there are families which existed before others'. But he went further, saying that in these successive families nature 'always improved them more and more, going from the simplest to the most complicated'.*

1794
PALLAS *found a woolly rhinoceros frozen in the soil of Siberia.*

1801–1809
LAMARCK *made the first clear pronouncement of the hypothesis of evolution, the derivation of one species from another. With the exception of Geoffroy-Saint-Hilaire nobody listened to him.*

1800–1812
CUVIER *basing his ideas on his law of the correlation of form, undertook the first methodical study of fossils. But he did not believe in evolution.*

1859
DARWIN. *'The origin of species.' From this time on the hypothesis of evolution was solidly based on facts. The palaeontologists began to reconstruct the family tree of the principal groups in the animal and vegetable kingdoms and their development in the course of time while demonstrating the direction and the detailed modes of evolution.*

1945
The dating of deposits, founded on the radioactive decay of certain atoms, made it possible to measure the absolute rate of evolution of species of animals and plants in millions of years. Species are now regarded as populations which can be studied both quantitatively and statistically.

a length of 60 feet and a whale 100 feet. For each epoch, the size of animals spreads around some average dimension, and if all obey the laws of probability, the greater the number of species, the greater the chance of any one being of a really large size. When we make calculations based on the Gaussian law of probability we find that, at least since Cambrian times, this has been the case. The law of increase in size certainly holds true but it is clearly related to the law of increase in the number of species.

More significant is the tendency towards complexity. Taking only vertebrates, the first fish without jaws appeared 420 million years ago; the first amphibian, 370 million years ago; the first reptiles, 320 million years ago; the first mammals between 230 and 160 million years ago. This order of appearance is precisely that of progressive anatomical complication and forms a classic proof of evolution, all the more convincing because it appears equally in every other phylum.

The diversification of species

We can think of the diversification that took place in the course of time in two ways. If the number of species increases, then that of different species must automatically increase. If the differences are simply in details—a shorter thorax or a red colour replacing a blue—diversification would signify no more than that. But if the differences are such as to affect the lives of the animals, they are of the greatest importance. The facts show that the latter is the case. The most conclusive proof of this is the fact that the most ancient fauna known, that of the Cambrian, is exclusively marine. Later, about 370 million years ago, definite land animals appeared for the first time and only later on, about 315 million years ago, do we find the first flying animals which were a type of dragon-fly. Thus, not only the details, but also the modes of life and the major outlines of animal form have become diversified in the course of time. The animal kingdom has little by little conquered all the many and varied parts of the earth and has not only diversified but spread. The different modes of life have increased in number and become more varied. For example, species which are commensal with the ants only made their appearance about sixty million years ago, when there were also ants. Thus life has undergone great changes in time, and basically in one direction.

But as we have seen, the actors themselves, the species, and the larger groups into which they fall, have changed. Have they been in some way independent of the main current?

The length of time the various kinds of groups have existed, for example the classes such as the birds, mammals, and so on, can be worked out and the median value for the series calculated. For a series of extinct classes, like the trilobites, one finds a mean value of 260 million years. For a series of classes with representatives still living, one might expect to find that they had been in existence for about half this time, since, on average, they should be about half-way through their life-span.

Paradoxically, however, we find that the duration is longer and at some 480 million years is almost doubled. It is the same for the next subordinate group, the orders: extinct orders show a mean period of 140 million years existence, while the surviving orders have already existed, on average, for 230 million years. The same holds for families, some 85 million years against 135. This seems to show that, for the classes, orders and families at least, the chances of survival were not the same for those which have become extinct as for those which survived. The extinct organisms were in fact only 'try-outs' which survived a shorter time. Those which still exist have established themselves and proved more durable: if one dare use the word, they have succeeded. Amongst them are the panchronic animals which have really proved themselves.

Going back along the ranks of the classification, the average length of existence for families still living is about 125 million years and for the orders about 230 million years, which is approximately twice as long, while for the classes the period is about 490 million years, which is twice as long again. It is tempting to attempt to go further back into the past, and on this doubling scale we find 1,000 million years for the phyla and 2,000 for the sub-kingdoms or kingdoms. This is still a matter of the average span. Some may have existed far longer. This fits into the scale of 3,500 to 4,500 million years assigned by radio-isotope measurements to the oldest rocks.

In conclusion, it is interesting to place man in this great evolutionary scheme of the animal world, which we have just sketched out. Tradition has presented him as the last-born, but recent progress in geology allows us to be more precise. At all levels our line falls among the younger groups. While, according to G. G. Simpson, a living species has a mean duration of two million years, ours, *Homo sapiens*, has only 50,000 years behind it. We have just scraped in and are lucky to exist at all.

The mechanisms of evolution

Michel DELSOL

Man's attempts to understand the history of life have themselves undergone an evolution, an intellectual evolution in which progress towards truth and understanding has been continuous if not constant. The history of this progress helps in understanding the significance of evolution for our own species.

G. G. SIMPSON

NOTE: *the passages enclosed between brackets in this chapter have been inserted for English-speaking readers by the editors of the English edition.*

Ever since biologists conceived the idea of evolution of living organisms they have tried to explain the determining causes and the mechanisms which have led to the formation of the genealogical trees they have drawn up. The need to understand showed itself long before the analytical description of evolutionary phenomena had made much progress, so that it is not surprising that the earlier Lamarckian hypotheses have now only an historical interest. It was only thirty years after the publication of Lamarck's *Philosophie Zoologique* that Darwin conceived the idea of natural selection, published twenty years later in his *Origin of Species*, and it was a hundred years later that de Vries discovered what he called 'mutation' (but which was a completely different phenomenon from that which geneticists define as mutation).[1] Since then biologists have had a wide base from which to work and a certain number of concepts from which they have been able to try and put together a comprehensive explanation of the march of evolution.

The researches which have been undertaken since have been carried out largely by zoologists, by palaeontologists and by geneticists (among whom the place of honour belongs to T. H. Morgan and his American colleagues). The first and second groups have been occupied in constructing genealogical trees of the living world and, at the same time, seeing to what extent the modifications, which they observe occasionally in their evolutionary genealogy, can be explained by mutation followed by selection.

The geneticists on the other hand have been trying, from the results of their laboratory observations and their theoretical calculations, to understand how the mutated descendants of a mutant animal which has appeared in a given population are able to conquer their place of origin and, sooner or later, replace the non-mutated, wild descendants which would otherwise have continued to occupy it. Based on the combination of these observations and the findings of palaeontology a new theory has been built up which is sometimes called Neo-Darwinism, but which it seems better to call the synthetic theory of evolution.[2] In contrast to the theories which have preceded it, the synthetic theory is not the work of one man.

It is the result of a considerable number of observations, a synthesis of the research of palaeontologists, biologists and geneticists conceived, little by little between the years 1920 and 1940.

The synthetic theory

According to the synthetic theory, the mechanisms of evolution work in the following way:

1. As a basis for the evolutionary modification there is mutation (followed by recombination of genes as a result of the working of the chromosome mechanism. This provides the heritable variation essential for evolution).
2. Natural selection only allows those animals best adapted to the conditions of their existence to survive (selection[3]).
3. In order that a new species can be created by this mechanism there must be a conveniently isolated habitat, so that the incipient species is reproductively isolated from its parent species (isolation[4]).

Mutation

It is well known that there exist in the nucleus of all living cells elongated objects which are called chromosomes and are made up by the stringing together of small units known as genes. The various genes secrete chemical substances which govern the formation of characters such as the colour of the eyes, the width of wings, the shape of the tail, etc. Under normal conditions the genes are self-reproducing and remain constant from

Drosophila is a small fruit fly which multiplies very rapidly. It is therefore a suitable subject for the biologist engaged in experimental work on heredity and mutations, many of which are very striking. For example, one fly may have long wings or atrophied ones, red eyes or white ones, a light brown body or a dark one. (See vol. 1, The Living Organism.) (Mag. × 40).

The cockroach ('black beetle') is the commonest of the panchronic insects which have survived without any essential modification for millions of years. (Mag. × 1·5. Photo Lod).

generation to generation. However, from time to time one or other of them undergoes a slight modification: it mutates. The character which such a gene governs is then changed to some extent in a direction which can be, according to the circumstances, favourable or unfavourable to the individual carrying it, and its descendants. In certain special circumstances among plants, duplication of chromosomes after hybridisation can concern the whole of the chromosomes themselves and in such cases a new species may arise almost entirely as a result of this single change.

But in general mutations only cause slight and imperceptible variations which may go unnoticed on superficial observation. (Nevertheless, they may play an important part as 'modifiers', for every gene affects all the other genes of the gene-complex of an organism.) The researches of geneticists appear to have shown clearly that the number of such small mutations is so large that given the whole duration of geological time they could have led to evolution. Simpson suggests that, taking the horse family, in the course of the fifteen million generations which make up their history, there must have occurred a minimum of one and a half million new mutations for each character of the teeth.

Selection

It is now necessary to consider how a mutated animal may find itself favoured or otherwise by its particular mutation, and it is here that we must introduce the concept of the struggle for existence, or natural selection, which it took the genius of Darwin to discover. (First of all it should be realised that, as Fisher showed, it is selection *not* mutation, that controls the direction and the speed of evolution: selection can also force evolution to stop when the conditions of existence of an organism remain optimal for a considerable time.) Certain mutations (and recombinations of genes) can bring the plants and animals which produce them very clear advantages, or disadvantages. In the course of their history the horses which could run faster had the best chance of surviving, the carnivores with the stronger teeth had the advantage when fighting, the peacocks with the brighter colours had the best chance of ensuring their perpetuation. Specialists in population genetics have been able to study the advantages of selection in the laboratory under controlled conditions. In a special 'population cage' one places a considerable number of *Drosophila* (fruit flies) made up of two sorts of individuals differing by a given mutation. For example, one might mix long-winged *Drosophila* with others bearing vestigial wings. These insects are given only a relatively small amount of food, insufficient for each larva to get enough to satisfy its needs. One finds that after several generations have been reared one of the two original types disappears. The ones with vestigial wings find it more difficult to survive than do the others, and in time they die out. (Under different physical conditions the results can be reversed,[5] which shows how all-important environmental conditions are.)

Isolation

When one tries to find out how living forms have given rise to new species the first explanation which comes to mind is that a new mutation has arisen at the same time in individuals of both sexes, whose mating has, by a lucky accident, given rise to a new race. In fact, it is not at all like that. It is now believed that in the majority of cases new species are formed through the isolation of a portion of a homogeneous zoological group. The most typical examples of this are provided by cases in which geographical isolation has occurred.

Let us suppose that a species of fish, which we will call A inhabits a lake, and as a result of geological upheavals the lake is divided into two parts which no longer communicate. Thus the mass of individuals which makes up the species A is now divided into two parts, which we will call A1 and A2.

It is inevitable that the two areas occupied by the populations A1 and A2 will differ in some respects. In each of the new lakes the

(1) A mutation *is the inception of a heritable variation and results from a change in a gene or a chromosome. What de Vries observed was the sudden reappearance of parental forms in hybrid plants of peculiar type.*

(2) *The integration of the Darwinian selectionist and the Mendelian geneticist points of view was achieved by Sir Ronald Fisher in his epoch-making work* The Genetical Theory of Natural Selection *(Oxford, 1930). The synthetic theory of evolution, embodying results of research in all fields of biology, was expounded in a general way by Sir Julian Huxley in* Evolution: the Modern Synthesis *(Allen & Unwin, London, 1942), and by G. G. Simpson in* Tempo and Mode of Evolution *(Columbia, 1944), and several later works.*

supply of food, the amount of light, the temperature, in other words the conditions in the struggle for existence and for natural selection, will not be quite the same. Furthermore, there will appear in each of the populations new mutations which will be different, as happens when we breed populations in the laboratory (and they will be subjected to selection in different directions).

After many centuries, millenia, or geological periods, the two populations A1 and A2, formerly exactly alike, will each have varied in a certain direction. Since the conditions differ and the mutations (recombinations and selection) have also been different, in each of the populations animals bearing different genes will have survived. Thus geographical isolation has given rise to two distinct types through its indirect effects and the two types, each evolving along its own lines, finally become sufficiently distinct to qualify as two species. (Examples of this actually occurring in nature today are provided by some species of gulls, tits and salamanders.[6])

What we have just said about species is true, to an even greater extent, of larger groups. In Australia which has been isolated from the rest of the world from very distant times, the first mammals evolved along special lines. They gave rise to a whole series of species which conquered every type of Australian environment and are widely different from those found elsewhere.

A difficulty that some palaeontologists found in considering the synthetic theory lay in the fact that the genealogical trees which they had constructed contain a very large number of discontinuities. Forty years ago the existence of these discontinuities was attributed simply to the lack of palaeontological evidence. It was expected that in time further researches by geologists would lead to the gaps being filled in, and this expectation has been increasingly well fulfilled. Thus Piveteau found in the Triassic strata of Madagascar a short-tailed fossil amphibian which filled in an existing gap, and the existence of some fossil intermediaries, such as the *Archaeopteryx*, and of several continuous lines of descent (reptiles—mammals) seemed sufficient to prove this hypothesis.

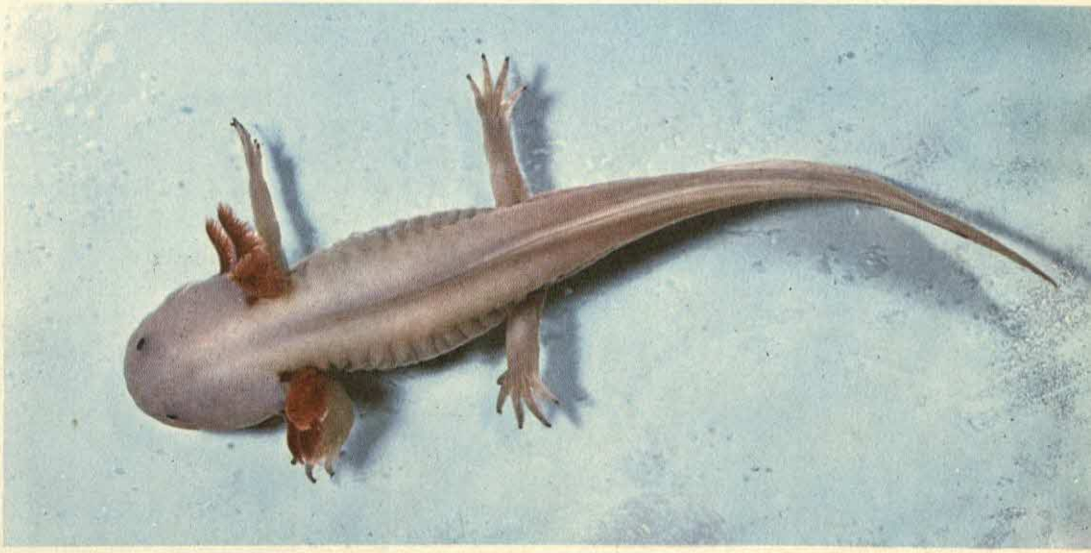
Nevertheless, some palaeontologists feel that the gaps in the palaeontological record are still too numerous for this explanation to be adequate in itself. Thus for all the thirty-two orders of mammals, the most primitive species already possess the fundamental characteristics of their order, but the palaeontological gaps which separate them are so great that even the origin of the orders is almost always conjectural.

There is another hypothesis, however, which might explain these gaps. It could be suggested that large-scale mutations have occurred which have led in some way to abrupt evolutionary leaps. If this were the case then clearly there would be no need to look for fossils of intermediate types. The synthetic theory offers another explanation, which is in many ways the most remarkable (put forward by S. Wright). It suggests that small isolated populations evolve much more rapidly than large populations, and this moreover seems to be borne out by genetical research. (This is known as 'genetic drift'.) The large evolutionary modifications, such as those which led to the appearance of the mammals, could occur rapidly in relatively small populations. From this it is logical to deduce that they would have left few fossils of the intermediate types and that, in the course of the important evolutionary changes, there would be large gaps in the genealogical trees.

These are some of the principles of the synthetic theory of evolution. Is this remarkable contribution enough to explain biological evolution? Does it succeed, a hundred and fifty years after Lamarck's inaugural lecture at the Muséum d'Histoire naturelle, in giving us the key to the evolutionary mechanism? The leading biologists in Great Britain and the United States think so; others are more sceptical, for reasons which we must now examine.

Criticism of the theory

No biologist today denies the important part played by the mechanisms of natural selection and mutation in the evolutionary



The axolotl is a batrachian which, according to circumstances, can either metamorphose normally or remain in the larval state. (Photo Lod).

---

(3) *The application of mathematical analysis to natural selection at the hands of Sir R. Fisher, J. B. S. Haldane, and S. Wright has made it possible to measure the pressure of selection quantitatively and to show that no mutation has any chance of establishing itself in the wild type of a population if even the slightest adverse selection is exerted against it. This is why selection,* not *mutation, directs evolution.*

(4) Isolation *may be geographical, genetical, or ecological, as Ernst Mayr has stressed.*

(5) *P. L'Héritier and G. Teissier found that wingless flies survive better than their normal rivals if a population-cage is exposed to an air-stream, again showing the paramount importance of selection.*

(6) *B. Rensch has drawn attention to the importance of the diversification of races in* Rassenkreise, *ring-species, which split into separate new species.*

process. Some however are still dissatisfied and think that the classic type of mutation such as we have observed in nature and in the laboratory is not sufficient to explain the building-up of the totality of characters which make up a living organism, even when aided by natural selection. The criticisms which are made of the synthetic theory are by no means a condemnation of the whole, but they suggest that the explanations it gives are inadequate. Those who raise them in fact refuse to believe that it is the final and complete answer.

Objections are raised against two distinct parts of the theory. Some suggest that selection by itself does not provide a sufficient sorting-out mechanism, others that mutation is insufficient to explain the development of new characters. The latter criticisms seem to be more convincing, so we shall deal only with them in this section.

The row of hooks which grip a ridge on the other wing of a bee present a simple example of coadaptation. (Mag. × 10).

The value of mutation

We must first deal with the problem of the number of mutations which occur in those species which we can call living fossils. If the classic mutation represents the essential factor in evolution we should logically expect that mutations would be rare in species which have changed little and evolved hardly at all over millions of years, the cockroaches, for example. Yet this is not the case; for the mutation rate seems to be as high in these groups as in others. The fruit fly *Drosophila*, is one of the organisms with the highest known mutation rate,[7] of the order of 1 in 1,000. 'If mutation were a variation of value to the species, then the evolution of drosophila should have proceeded with extreme rapidity. Yet the facts entirely contradict the validity of this theoretical deduction; for we have seen that the *Drosophila* type has been known since the beginning of the Tertiary period, that is for about fifty million years, and it has not been modified in any way during that time. If we recall that during this same period the whole evolution of the mammalia has taken place it can be supposed that *Drosophila* is a very stable type of animal and that a theory of evolution based on the study of a single species so stable in its organisation is ill founded'.[8] (British and American biologists are not worried by this because they believe that it is selection and not mutation that controls the speed and direction of evolution.)

The problems of coadaptations

The problem of coadaptations[9] seems to some biologists even more difficult to resolve. It is well known that many animals possess specialised parts which can be compared to tools. The suckers of some parasitic worms, and the ovipositor of insects are simple examples of this. There are also more complicated tools which can be called coadaptation tools because they are made up of two or more independent parts of different morphological origins, each forming a section of the tool. The anterior edge of each hind wing in a honey bee has a row of small hooks which catch over a ridge on the hind edge of the front wing. In the cuttlefish there is a protrusion which fits into a cavity beneath it rather like a press-stud.

Examples of this type of thing are very numerous in nature and give the impression that one of the parts of the organ showing coadaptation has led to the moulding of the other, or has itself become adapted to the other. The fact of coadaptation seems indeed to be a very general one among living organisms. Can we not look upon the brain and the sense organs as showing coadaptation to each other? Certain biologists have chosen to see in this type of organisation a sort of finality in nature, but it does not seem very profitable to enter into this debate here. It is nevertheless true that these tools made up of several distinct parts, each independent of the other, cannot very easily be explained by the interplay of mutation, since this would imply that several chance mutations at the same time had led to the formation of the different parts of the organ. At first sight this might not seem impossible, given the abundance of possibilities for mutation, which is in the order of 1·5 million mutations for each slight change in the teeth during the volution of the horse, as already mentioned. But there is a very considerable difference between the probability of one mutation appearing at a given point and that of several mutations conveniently appearing in the same or adjacent places, so as to lead approximately at the same time to the formation of a co-ordinated organ formed of different parts. The laws of chance show us that the probability of such an occurrence is very remote indeed. One could of course suggest another hypothesis, that one mutation could lead to the appearance of the other parts of the organ at the same time, but this would be even more extraordinary. (On the other hand, if selection controls the effect of mutation, as the experiments of R. A. Fisher, E. B. Ford and others have shown, there is less difficulty in understanding how correlated variation occurred.)

(7) Mutation rate. *The rate of normal mutation has been estimated in some bacteria, plants, animals, and man. It is of the order of one mutation for every half-million gene-loci per generation. Every individual, of course, has many gene-loci in its chromosomes.*

(8) *Quoted from A. Vandel:* L'Homme et l'évolution *(Gallimard, Paris, 1958).*

(9) Coadaptations *or correlated variations, involve the parallel development and modifications of two complementary structures, such as the eye-cup and the lens which arise from different rudiments. Studies on organizers in experimental embryology have proved in many cases that the two structures involved in coadaptation fit harmoniously because one induces the formation of the other, in the appropriate place and size.*

(10) *Quoted from P.-P. Grassé:* Paléontologie et Transformisme *(Albin Michel, Paris, 1950).*

(11) *Quoted from Fontaine:* La vie aérienne des poissons *(Revue scientifique, 1950).*

The mystery of convergence

There is another difficulty which some consider as the most important of all. If the evolution of organisms comes about by the random chance of mutation and selection, there would be very little probability that complicated mechanisms would be formed several times at several different points on the genealogical tree. Yet in fact biologists have often come across such similarities. In the simplest cases they are called convergences, but in general the more complex cases have been little studied except perhaps to expound certain unacceptable philosophical views, such as vitalism. It is well known that a complex eye, constructed according to a very similar anatomical plan, is found in both the cephalopod molluscs like the octupus and the vertebrates. Among the higher vertebrates it appears that the mechanisms enabling the organism to maintain a constant temperature is different in birds and mammals: it is also conceivable, according to some palaeontologists, that this capacity was present in some reptiles living in the Mesozoic era.

The capacity to maintain their offspring in an internal cavity during early development has appeared seyeral times in the vertebrates. At first sight it would appear likely that the various methods by which this is brought about are completely independent of one another and result from simple convergence, without it being necessary to seek any closer connection between them. However, one fact, at least, is very curious. In the species of frog known as *Nectophrynoides occidentalis*, which is found in West Africa, and has been described and studied in detail by Maxime Lamothe, the tadpoles develop in the uterus and the animal, unlike other batrachians, is born after metamorphosis, in its adult form. Gestation lasts eight or nine months. Now during this gestation there exist in the ovary certain bodies which seem to resemble the corpus luteum which is so prominent in mammals during this period. (The corpus luteum, or 'yellow body', is formed in the ovary from the egg-follicle after the egg has been expelled.) In each case the corpus luteum in the ovary prevents the maturation of further ova. In each case the maintenance of the pregnancy and the birth of the offspring coincide respectively with the maintenance and regression of this corpus luteum which may very well secrete the same hormone, progesterone.

It is easy to imagine that the interplay of mutations could have led, in several zoological groups, to the appearance of mechanisms for the internal development of the embryo, but it is difficult to believe that in two separate and totally divergent lines of vertebrate evolution there would be formed quite independently in the ovary an hystologically rather similar endocrine organ designed to accompany and to regulate those mechanisms which perhaps secrete the same hormone. Although Lamothe has adopted the synthetic theory to explain these facts, it seems unthinkable to some that the interplay of mutations alone could twice have led to the formation of such similar bodies.

Here again of course one might suggest that these phenomena can simply be explained in terms of the possibilities of mutation which we have already discussed. However, when a complex mechanism is set in motion by simple chance, if it is to reproduce the same pattern twice it needs a number of possibilities very much greater than can in fact have occurred during the known extent of geological time. (British and American biologists would agree, again because they hold that mutations by themselves achieve nothing; it is selection that controls evolution, and selection exerted in similar directions from different starting points results in parallel evolution and analagous results.)

A common genetic stock

Yet other hypotheses come to mind which might explain these phenomena. It might be supposed 'that living matter has at its disposal only a limited number of solutions to the same problems, a condition which is favourable to "coincidences". This however is an unverifiable theory which greatly reduces the evolutionary potentialities of the living organism.' Or it might be 'that the groups under consideration, since they possess a common genetic stock, must show similar variation within a group of characters'.[10]

Certain experiments suggest that there may be some truth in this latter hypothesis. We sometimes get the impression that we only need one hormone, one enzyme, to make evolution advance in a particular direction. For example, thyroxine behaves like the hormone for emergence from the water. There are fish which live for a major part of their lives out of the water. These are the Periophthalmia, some species of which are more aquatic than the rest. 'Now Harms has taken species of Periophthalmia which are little adapted to life on land, such as *Periophthalmus chrysopilos*, and *P. schlosseri*, and treated them

(12) Macromutations, *hypothetical sudden large changes, invoked by some biologists to account for still unfilled gaps in the fossil record and for the origin of higher taxonomic categories, eg, genera, without passing through the series of minute selected variations that produce races and species. Macromutations have less and less hypothetical basis as palaeontological discoveries increase, and they are rejected not only by palaeontologists like G. G. Simpson and geneticists such as Sir R. Fisher, T. Dobzhansky, and E. B. Ford, but by general biologists like Sir J. Huxley and B. Rensch.*

(13) *A. Giard drew attention to this fact many years ago.*

HISTORICAL NOTES

Before 1800

Several philosophers and naturalists tried to explain the origin of the living world by an evolution of species, but no overall picture, and especially no explanatory theory, emerged from their speculations.

11 May 1800

LAMARCK, *who held the chair of 'Invertebrata' at the Museum of Natural History in Paris, in the course of his inaugural lecture first traced the broad outlines of his theory. He published his* Philosophie Zoologique *in 1809 and suggested that evolution is brought about by the moulding action of the environment on living organisms. Changes in the environment led to changes in the form of organs. The characters thus acquired were then supposed to be inherited.*

1831

DARWIN *began his world tour, during which he made the observations that led him to the idea of natural selection.*

1858

DARWIN *and* WALLACE *published their joint paper on evolution by natural selection.*

1859

DARWIN *published* The Origin of Species. *In this work he showed that the various individuals descended from a single*

Continued on page 37

with thyroid hormone. He has seen these animals leave the water, pass several hours on dry land, become progressively more like amphibians, and even more striking, take on the morphological characters of the species *Periophthalmus argentilineatus* which is normally the most pronouncedly amphibian of the group. Harms has even been able to produce amphibian behaviour in a typically marine species *Blennius ocellatus* by feeding it thyroid. This blenny came right out of the water, showed an aerial type of respiration for eight hours uninterruptedly, then slipped into the water for a short time before resuming its position for several hours more on a stone which was completely dry. He has thus been able to change the behaviour of a species experimentally by a hormone, a result which appears to me of great interest'.[11]

The stumbling-block of evolutionary jumps

But another difficulty remains. Simpson and the other supporters of the synthetic theory of evolution believe, as we said earlier, that the interplay of the smallest mutations is enough, through the action of the laws of genetics and selection, to explain the gaps in the family trees of the thirty-two orders of mammals without evolutionary jumps or macro-mutations.[12] Here there seems to be a question of psychology; for the opponents of the theory are most concerned with the gaps. The explanation of rapid evolution in small populations does not satisfy them and they look for evolutionary jumps, giant mutations which would speed up evolutionary progress from time to time. The supporters of the synthetic theory, on the other hand, who believe that their evidence is sufficient to make their conception a complete and coherant whole, reject the principle of evolutionary jumps. (In this they are supported by the distinguished German biologist B. Rensch and others, who reject the possibility of giant mutations on numerous grounds.)

It has often been observed in nature that important modifications may occur which are not hereditary but which show that the same individual may appear with different morphological characteristics in a different environment. All biology books mention the morphological changes in plants from the valleys which have been transplanted to alpine regions, or the changes which occur in the crustacean *Artemia salina* with variations in the salinity of the water, and there are other examples which are even more striking. *Proteus*, an amphibian living in caves, normally lays eggs, but when the conditions become unfavourable for their development through lack of food or rise of temperature, the animal produces its young alive. The story of the axolotl is even more curious. During the expedition to Mexico which took place at the time of the second French Empire (1862–67) General Forey sent the Muséum d'Histoire naturelle in Paris a Mexican amphibian which was unknown at that time. The animal was given a Latin name, as is customary for all the new species which are found. Now, one day the descendants of these amphibians which were still living in the Museum, underwent a metamorphosis and became transformed into an animal already known and described which bore the name *Amblystoma mexicanum*, a type of salamander. A study of the phenomenon showed that the axolotl is an amphibian which can, according to circumstances, either metamorphose normally or remain permanently in the larval state and in either case it can reproduce as if it were adult. The difference between the two forms is so great that if they are seen separately it is impossible to guess that they are the same animal.

Clearly, therefore, one organism may during its existence appear in two forms, and thus the morphological description of a species is less absolute than is generally believed.[13]

In order to explain the evolutionary jumps which occur in the genealogies and which the synthetic theory appears not to deal with adequately, the embryologist Dalcq has put forward the idea of giant mutations which would have their effect on the embryo and could therefore produce much more extensive effects than can the mutations we have dealt with up to now. These have been called 'onto-mutations', and the reply to such suggestions is usually that they are purely imaginary and that it is difficult to postulate mutations of a kind never yet observed. But is this criticism not also true of the hypothesis which explains the gaps in the family tree separating the thirty-two orders of mammals from their common source, by postulating an especially speedy evolution in certain populations?

Many biologists today believe that in the synthetic theory of evolution we have the key to evolutionary mechanisms. Personally, however, I do not feel that the several explanations put forward by this theory are enough to explain the whole of evolution. It has certainly produced a number of new explanations, but it still leaves too much unexplained for us to consider the debate on evolution closed.

Continued from page 35

species always present small variations which are inherited. After selection by the effects of the environment and the struggle for existence only those which carry favourable variations survive. Contrary to what Lamarck believed, the environment has only a passive role: it selects.

1865

MENDEL *discovered the particulate nature of heredity and demonstrated its laws.*

1900

The work of MENDEL *which had been ignored was rediscovered and independently confirmed by* H. DE VRIES, C. CORRENS, *and* E. VON TSCHERMAK *in plants.*

1902

W. BATESON *and* L. CUÉNOT *established the fact that Mendel's laws of heredity apply to animals.*

1919

T. H. MORGAN *published his theory of the gene in* The Physical basis of Heredity, *giving irrefutable experimental proof that chromosomes are the bearers of genes.*

1928

H. *J.* MULLER *induced increased mutation rates in organisms by radiation.*

1930

Sir RONALD FISHER *published* The Genetical Theory of Natural Selection, *integrating Darwinian selection with Mendelian genetics, showing that particulate inheritance conserves variance, and that the effects of any gene are conditioned by the other genes of the gene-complex and subject to the effects of selection on recombinations of genes brought about by the chromosome mechanism.*

1938

T. DOBZHANSKY *and* A. H. STURTEVANT *demonstrated the sequence of derivation of some species of* Drosophila *from the structure of their chromosomes.*

1942-1944

Sir *J.* HUXLEY *and* G. G. SIMPSON *integrated genetics with ecology, taxonomy and with palaeontology in their synthetic theories of evolution.*

Musing on evolution

Rémy CHAUVIN

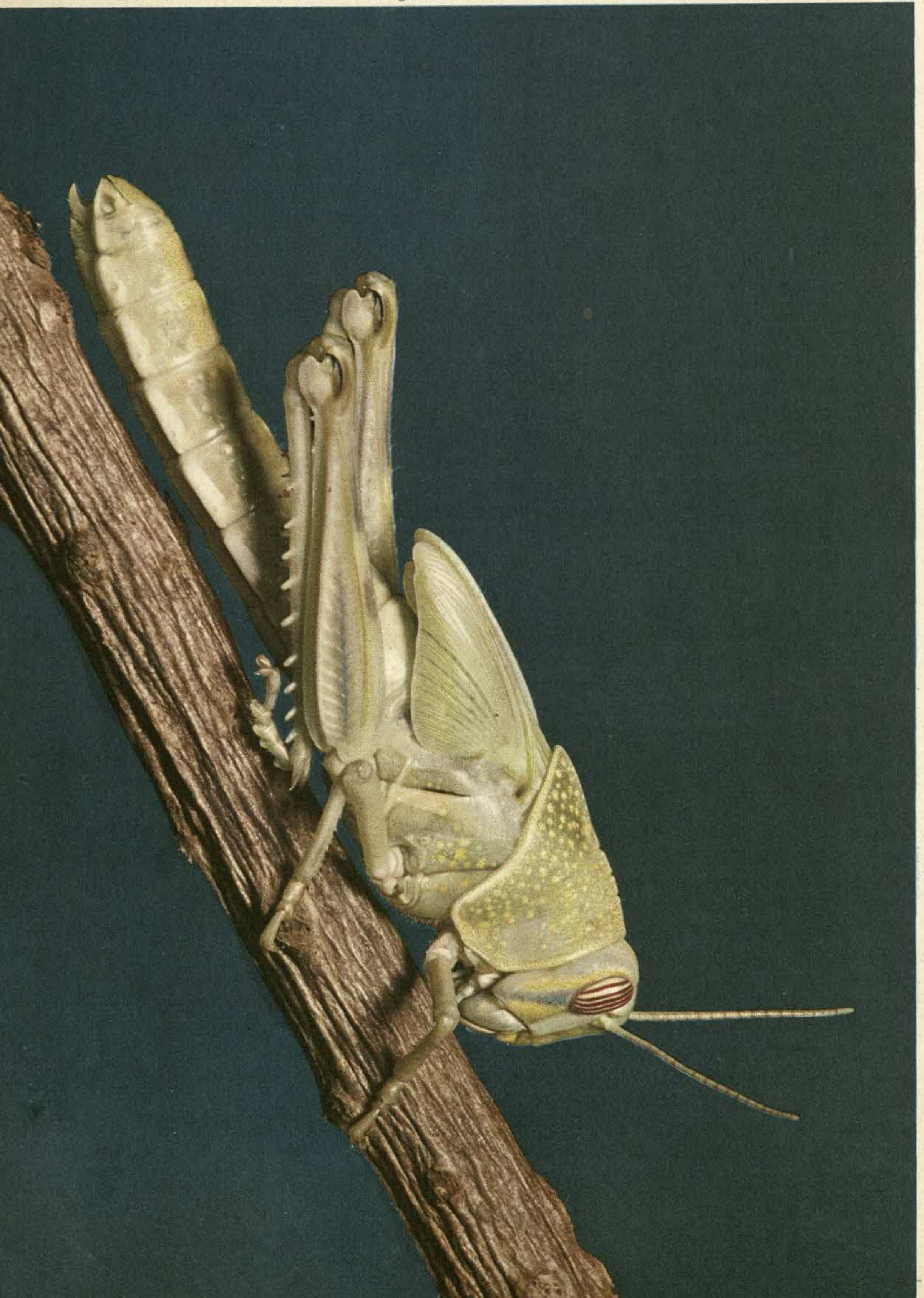
The history of biology clearly shows that for too successful theories the Tarpaeian rock, the place of execution, is close to the Capitol. An excellent example is provided by experimental psychology which, twenty or thirty years ago, explained everything in terms of conditioned reflexes or tropisms, and although everyone acknowledges that these theories have illuminated a large number of phenomena, there remain just as many which, disdainfully ignored by the fashionable theorist, are as obscure as ever. Oversimplification brings about as many problems as it solves. This is such a frequent occurrence in the history of science that it is an almost self-evident truth. If the latest theory throws a vivid light on some of the problems of life, it does so at the expense of others which are conveniently forgotten.

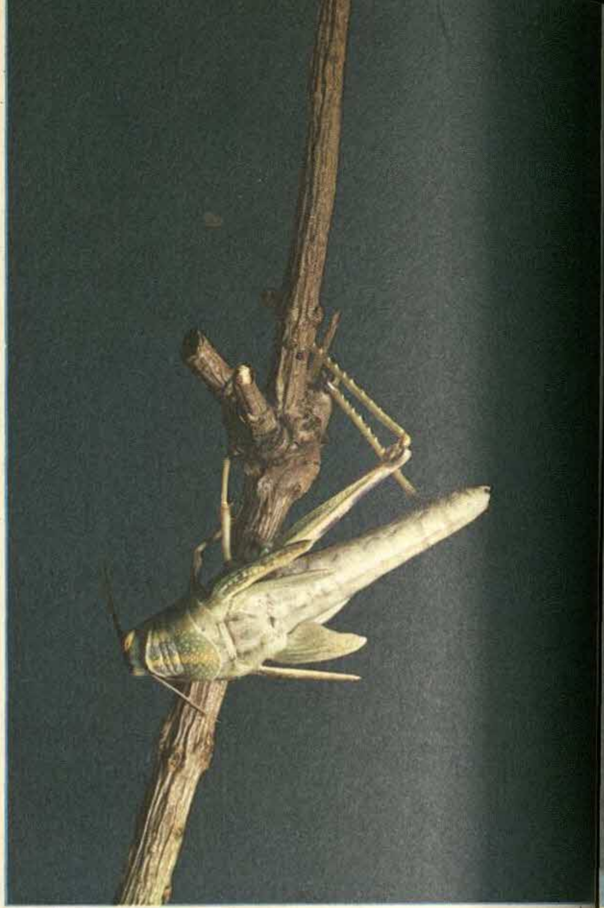
However, it is unfair to say, as does one well-known biologist, that all these evolutionary theories are no more than old wives' tales, which people merely pretend to believe. On the contrary, their value in explaining things has to be recognised. Michel Delsol, in particular, has made this very clear.

Opposite page:
The Collembola, primitive wingless insects which live in the soil, have remained practically unchanged for hundreds of millions of years, despite their frequent mutations. (Mag. × 90. Photo Lod).

The locust moults

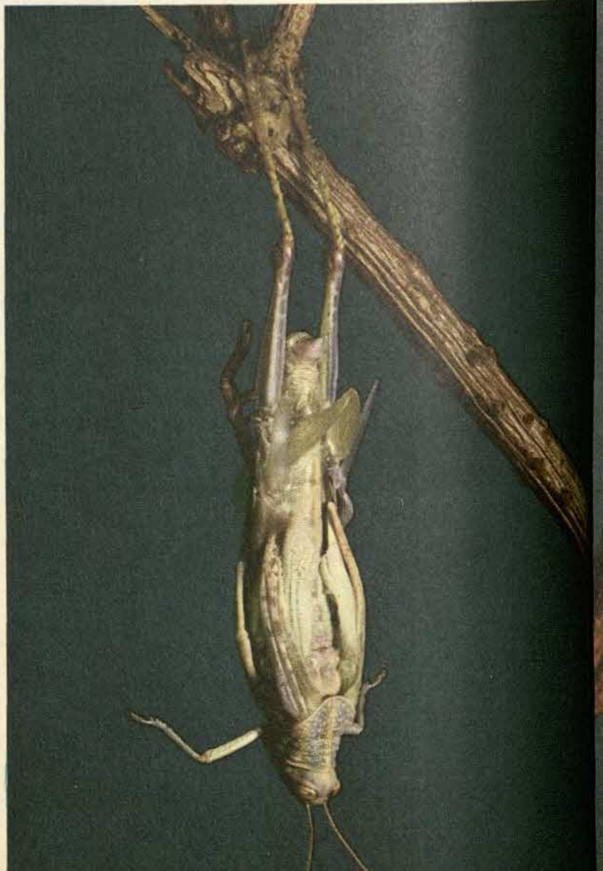
The locust is the typical example of insects with incomplete metamorphosis. It passes direct from its larval state to its adult form (or imago) without forming a chrysalis but undergoes a succession of moults. The photographs on this and the following pages show the sequence of a complete moult in the desert locust, Schistocerca gregaria *(Forsk). The moult takes about three-quarters of an hour. All the individuals shown here about life size, or slightly magnified, are the solitary form, light green in colour, except for three of a brown colour which are the gregarious form. This unique film of a metamorphosis, photographed at each intermediate stage, has been made with the help of F. O. Albrecht, Maitre de recherches, at the Laboratoire d'Evolution des Etres Organisés, Paris.*

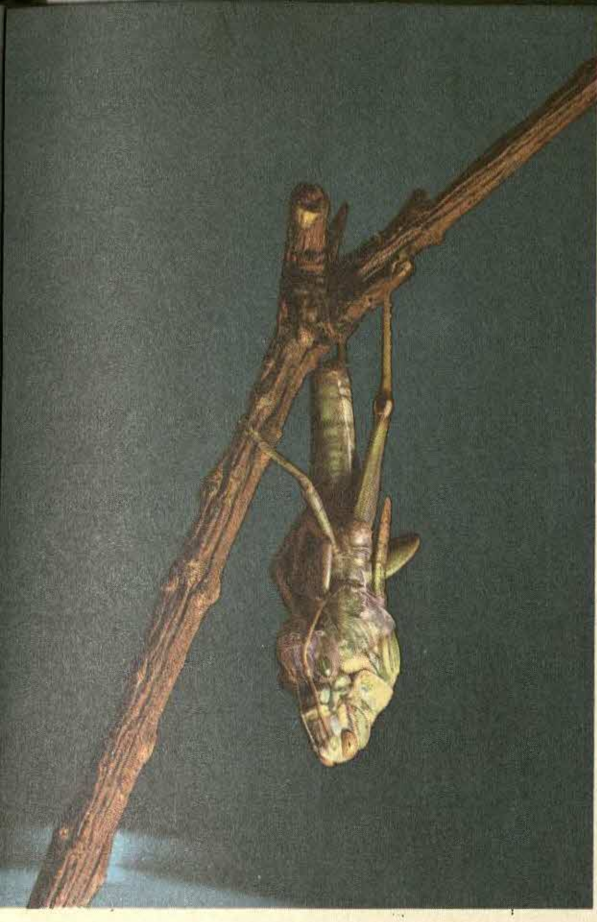




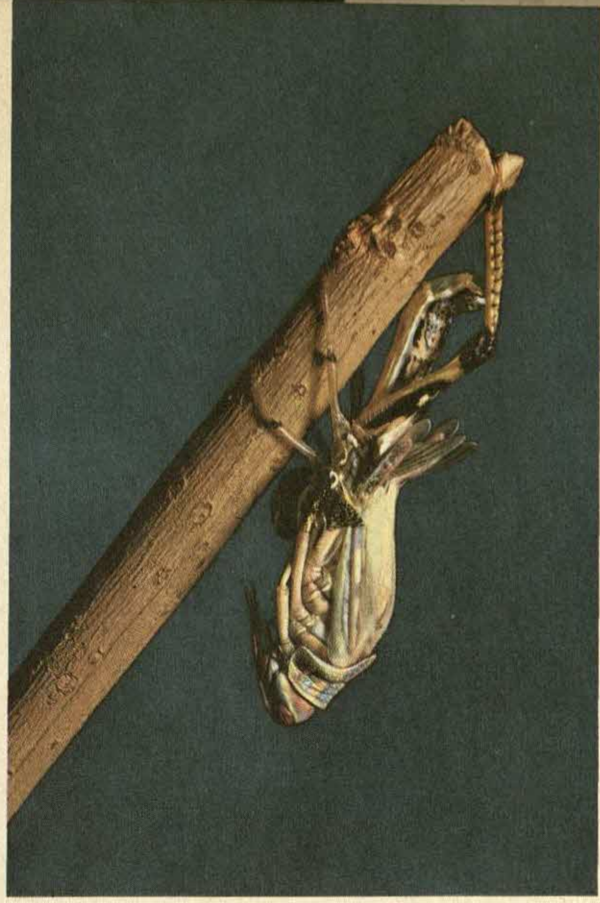
At the time of the moult the insect (left) fixes itself to a branch head down. Under the action of gravity it will escape little by little from its old skin. (Above) The animal grips its support, the wing buds separate and the skin cracks over the middle and end parts of the thorax.

A solitary form seen from the back. The front limbs and the wings can be seen after their emergence.

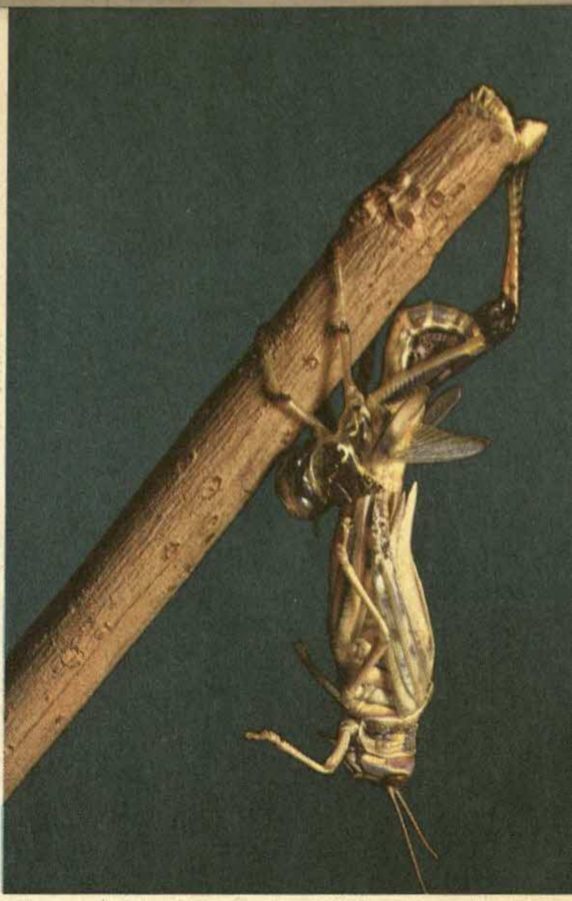




The actual moult has just begun. Head, antennae and prothorax escape from the old skin.

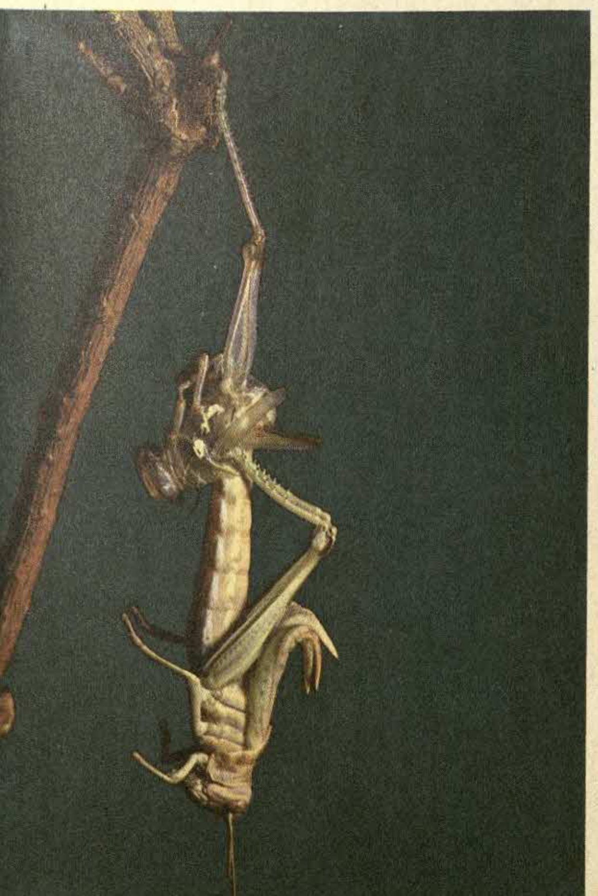


A gregarious specimen of the same species. The wings and front legs are emerging from their envelope.

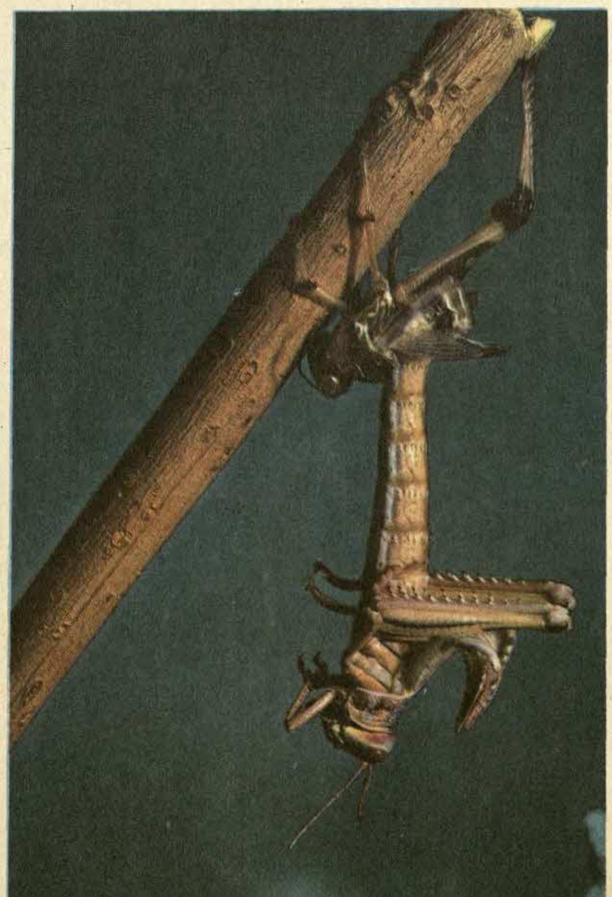


The same specimen, but by this time the front legs and wings are completely free.

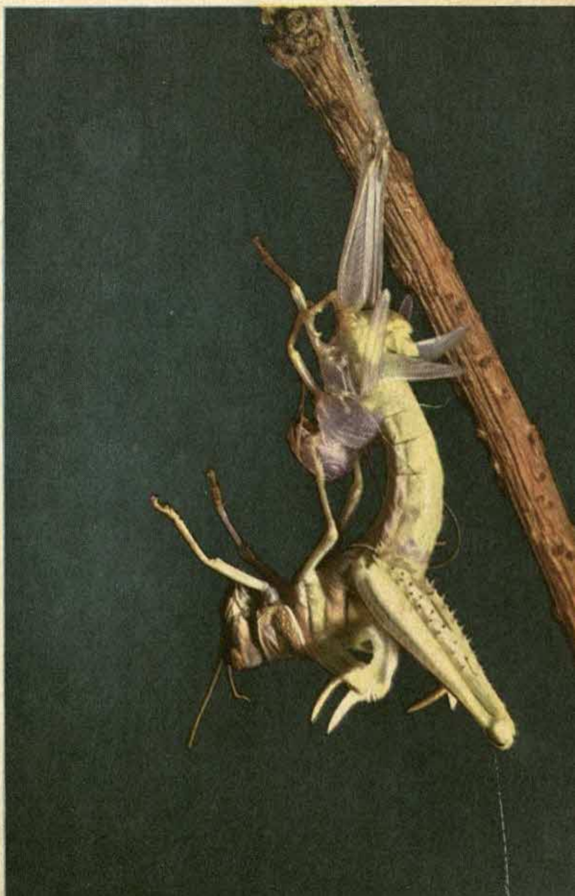
The same specimen, by this time the back legs are almost free.

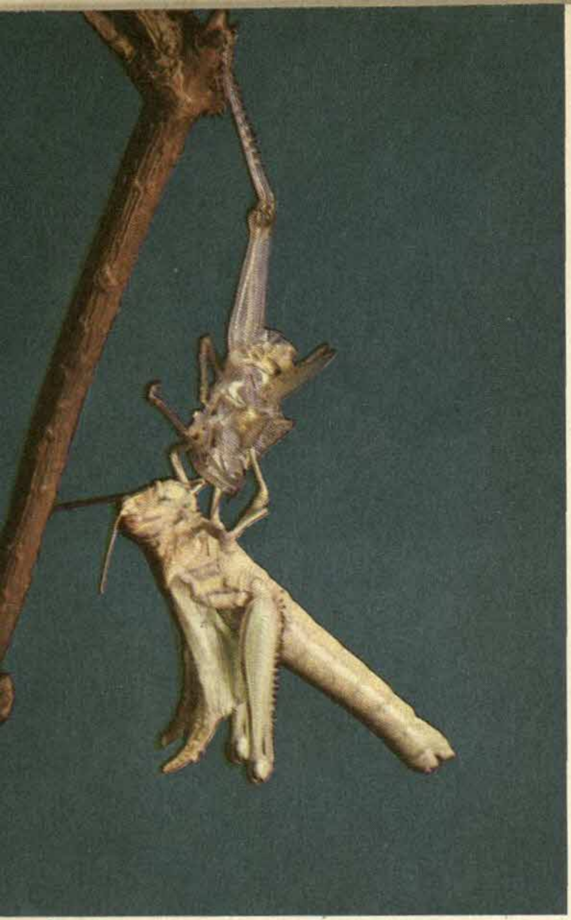


A gregarious specimen. The back legs and wings are free but the wings are still soft and curved back.

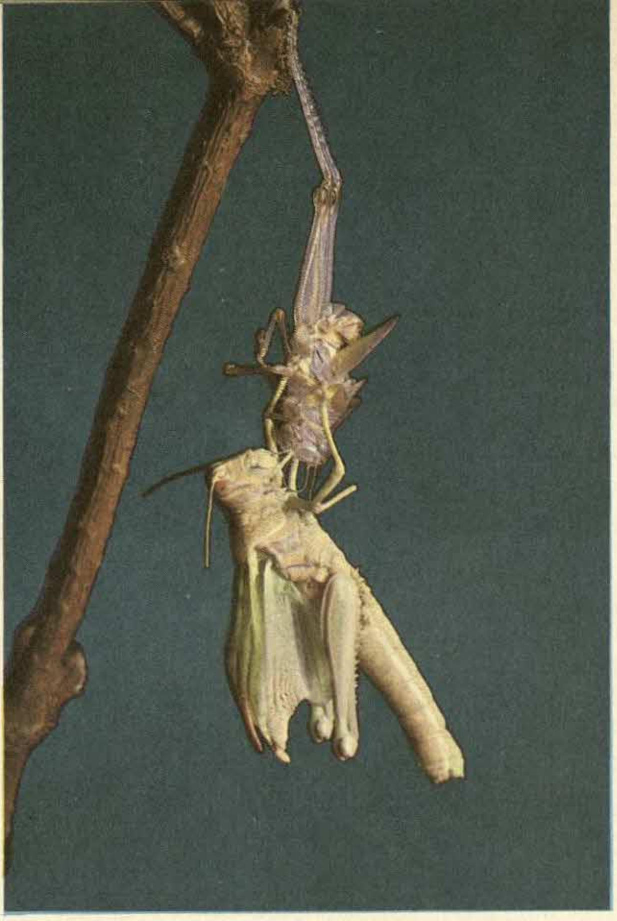


This is the crucial moment of the moult, the turning round. The insect makes an effort and grips its old skin. The white threads are the old linings of the tracheae or breathing-apparatus which are left behind with the old skin. Metamorphosis causes internal rearrangements.

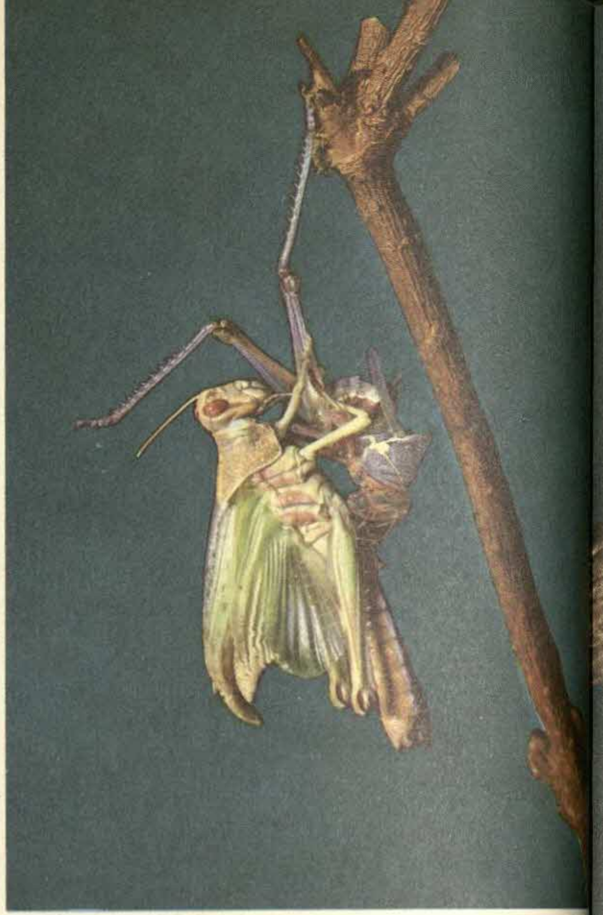




Gripping its old skin the animal is preparing to extend its wings.

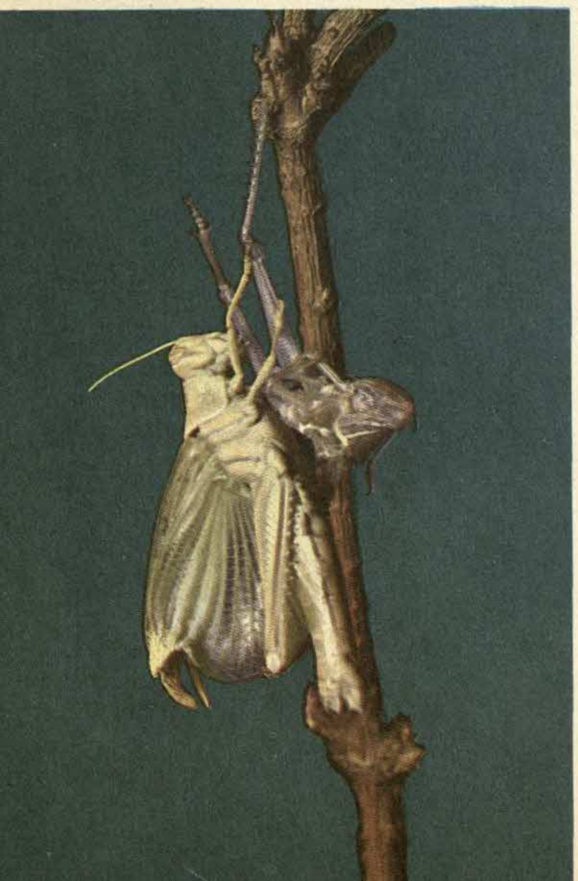


These are the last moments of the moult. The wings begin to unfold.

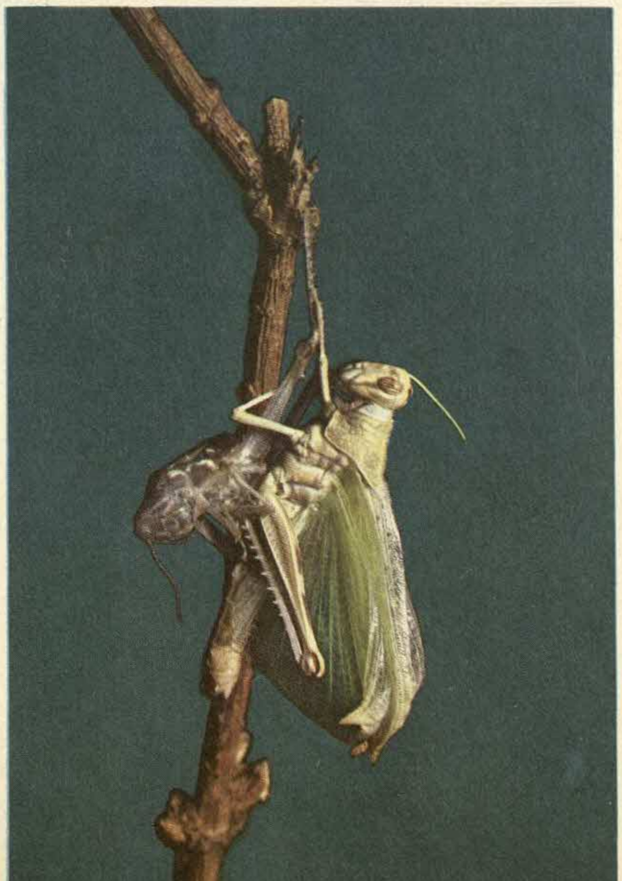


The wings unfold further and begin to elongate.

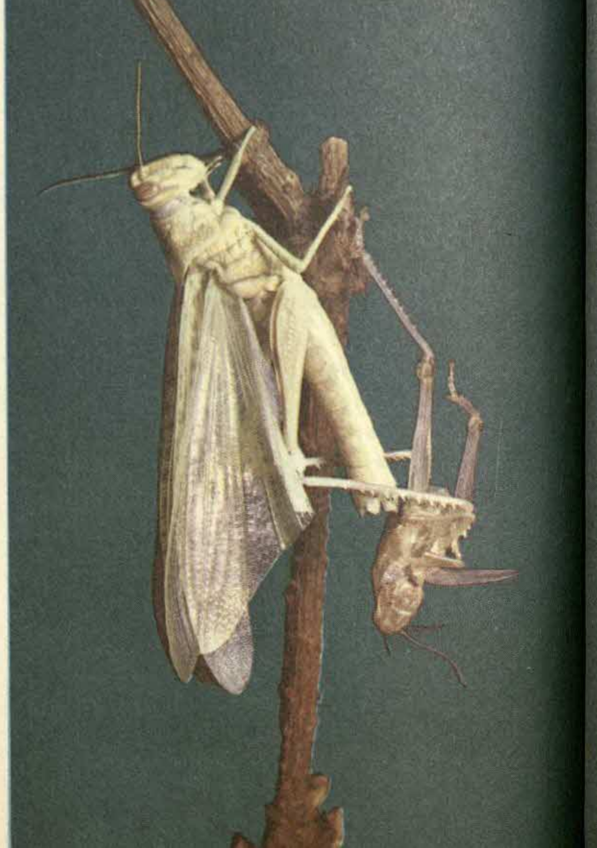
The wings spread out, showing their structure as they become transparent.



The locust leaves its old skin to grip the branch itself.



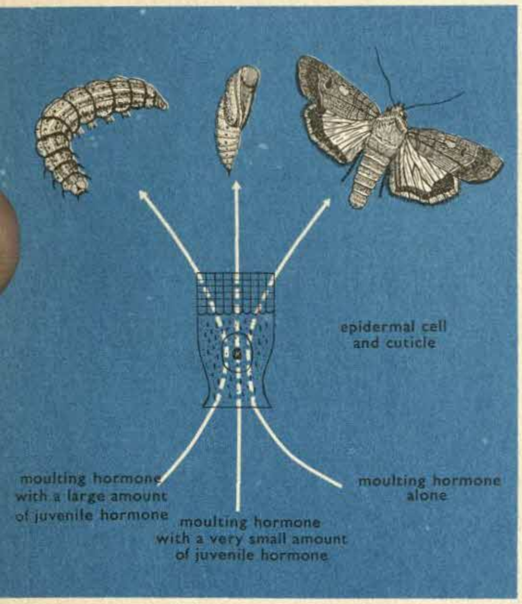
The wings are now straight and be to close up. The last picture shows final stage, greatly enlarged. T wings have taken up their norm position. The moult is finished and imago is ready to lead an adult li



Metamorphosis

Vincent B. WIGGLESWORTH

The young of all animals differ in varying degrees from the adults of the same species. The lion cub is a soft and furry creature with vestiges of stripes like a tiger; the young frog is a tailed and legless tadpole with gills for breathing under water like a fish; and the caterpillar is even more unlike the butterfly into which it will develop.



The form of the insect is determined basically by the formative epidermic cells of the cuticle. This diagram shows how their activity is controlled by the hormones regulating metamorphosis.

No one would doubt that the lion cub has the same body as the full grown lion it will become. But in many insects the transformation from the grub or 'larva' to the winged perfect insect or 'imago' is so spectacular that the change was termed by the ancients 'metamorphosis'.

When the larva is fully grown it turns into a chrysalis or pupa. In this state the substance of its body was believed to dissolve into a formless pulp and then, by some mysterious process, to be remoulded into the adult form. William Harvey, famous discoverer of the circulation of the blood in mammals and man, compared the production of the adult insect with the moulding of wax by the impression of a seal.

This mystical conception was brought to an end by the discoveries of the Dutch naturalist Jan Swammerdam, which were published in 1669, nearly twenty years after Harvey's death. Swammerdam stripped away the outer skin or cuticle from a caterpillar that was approaching the time for metamorphosis and found the vestiges of the wings already in process of growth. He concluded that 'metamorphosis', in the mysterious sense in which the word had been used in the past, did not exist. He maintained that growth in insects, as in all other animals, is an orderly process in which the body of the adult is produced by the development of structures already present in the larva.

Today we use the word metamorphosis simply to describe the extreme and often abrupt change in form which many animals, and particularly insects, undergo when they reach the adult stage. But the problems of metamorphosis are just as difficult today as they were in ancient times.

Enigma of metamorphosis

These problems are of two kinds. The first concerns the origin of metamorphosis. How has it come about in the course of evolution that one and the same animal can be either a caterpillar or a butterfly? The second problem is of a different sort. Accepting the existence of metamorphosis, by what physiological means is the change of form in the body regulated and controlled?

One explanation of the origin of metamorphosis, which is still accepted by some authors today, goes back to William Harvey and indeed to Aristotle. According to this idea the insect larva is really an embryo. 'The larva while it is yet in growth', wrote Aristotle, 'is a soft egg'. Harvey developed this idea further by supposing that the insect egg contains so little yolk that the embryo is obliged to emerge before its development is complete. It then goes through a more or less prolonged larval stage during which it stores up quantities of food material—more yolk, as it were—before resuming the egg form or pupa and completing its embryonic growth.

This was an attractive idea because it seemed to provide a satisfactory explanation for the amazing transformations which insects undergo. And some colour is lent to the idea by the fact that the outward form of the body of the larva is often rather simple, whereas the form of the adult is commonly much more elaborate.

But this is only a superficial impression. A caterpillar is not a simple animal. It has an elaborate internal anatomy, with many more separate muscles than we have, and an elaborate nervous system; it is able to live a free life and maintain itself successfully in a hostile world. The maggot of a fly or the grub of a beetle or bee is equally complex in its own way. Indeed, each of these insect larvae is a highly complicated animal, closely adapted to its own way of life.

A line of evolution

Herein lies probably the key to the origin of metamorphosis. Metamorphosis is the logical outcome of a particular line of evolution.

One of the most primitive sorts of insect still in existence today is the firebrat, *Thermobia domestica*, a wingless creature with long sensory antennae in front and sensory tail filaments behind, which is often abundant in warm bakeries. In its general form this insect is believed to resemble some of the earliest kinds of insects that appeared on the earth. In the course of its life it shows very little change in outward form; all its stages are alike. And that is not surprising, for young and adults all live the same type of life together, in exactly the same surroundings.

The firebrat is exceptional among insects in that it becomes sexually mature before it is fully grown. In most insects (as indeed in most animals) growth ceases as soon as sexual maturity is complete. In such insects the needs of the larva may be very different from those of the adult. The larva must feed on a rich enough food in order to grow and to store up within its body all the reserves that will be required to complete its transformation into the adult. The prime need of the adult is to find a mate and to breed. It must be active and mobile. While the larva is browsing on the leaves or burrowing in the stems of plants or feeding on the excreta of large animals or in their decaying bodies after death, the adult may be moving rapidly from flower to flower.

Role of natural selection

Under these circumstances natural selection will favour different characters in the larva and in the adult. The sort of body that will be best suited for chewing leaves or burrowing in the carcasses of animals will be very different from the sort of body required for flitting from flower to flower and seeking a mate. In other words, the larva and the adult have evolved independently and in different directions to produce two different sorts of organism, each closely adapted for its own way of life. And, where the environments that are occupied by the larva and the adult are very different, these too become totally unlike in form and habit, until we reach the extreme difference between the maggot and the fly.

In some insects, certain beetles for example, the larva may resemble a primitive adult insect; it is the adult alone which has become specialized. In the fly and in the bee the larva has become a maggot—outwardly appearing simple or degenerate, but really highly specialized. A different sort of specialization is seen in the caterpillar of the butterfly.

In most insects, where there are these striking differences between larva and adult, an intermediate stage or pupa has evolved which takes no food and merely serves to bridge the gap in structure between the two. In the dragonfly, however, there is a spectacular metamorphosis from an aquatic larva to a winged adult with no resting pupal stage.

In other insects the young stages have evolved along very much the same lines as the adults. The grasshopper that hatches from the egg lacks wings and sexual organs, but it is none the less quite obviously a diminutive grasshopper. The same is true of the bugs, insects which suck the juices of plants or the blood of other animals. Even in these kinds of insects, however, there is a far more striking change in form at the final stage of growth when the fully winged adult is produced than at any of the earlier stages. They also undergo a metamorphosis, and the more closely they are examined the more striking this metamorphosis is found to be.

We may summarize the argument thus far by saying that metamorphosis occurs because the larval form, the pupal form, and the adult form have evolved independently of one another to suit different environments, and are inherited independently.

Polymorphism, genes and metamorphosis

Looked at in this way metamorphosis has much in common with 'polymorphism'. All

The Lepidoptera go through a complete metamorphosis: larva, chrysalis or nymph, and adult form. Here is the chrysalis of a tropical butterfly, magnified three times. (Photo Lod).

A female cricket (Schistocerca septemfasciata) *laying eggs. The abdomen has hollowed-out a canal in the tube of earth, at the bottom of which one can see the eggs as small rods of a yellowish colour. The attitude of the male, who is gripping the laying female, is characteristic. (From the Laboratory of Prof. F. O. Albrecht. Photo Lod.).*

animals are more or less 'polymorphic'. That is, within a single species there are a number of recognizable forms. Perhaps the most familiar are the male and female forms, which are often strikingly dissimilar within a single species. But there is an endless number of other variants. These differences in form are controlled by the genes of heredity; and, since a single gene often has multiple effects, a single gene change may produce large differences in general form.

Now according to classical Mendelism the form of the animal is determined by the balance between the genes which it carries in its cells. But in practice there are many examples where the balance between the genes can be upset by other factors. Some genes in insects produce their effect only if the animal is exposed to cold, others only if it is kept unduly warm, and yet others only if the food is deficient in certain vitamins. Insect parasites feeding within the body of a certain insect develop a characteristic form, but if they develop within a different insect, and thus perhaps receive different nourishment, they may develop into a different form, so unlike the first that they could be thought to belong to a different species.

The balance of the genes which control sex can be upset in a similar way. Certain solitary bees and wasps may have their sex partially reversed if they are invaded during their larval life by the strange parasitic insect *Stylops*. Male bees develop the form and markings of female bees, and female bees acquire the characters of males. Here again the immediate cause seems to be an effect of the parasite on nutrition. One must suppose that when the growing organs and tissues are deprived of some essential factor in nutrition, then the gene balance is upset and the latent genes of the opposite sex, which would normally be suppressed, are able to exert their action.

The most rational way of thinking about metamorphosis is to regard this as just a special example of polymorphism in which the different forms, instead of appearing in different individuals of the species, occur as successive stages in the development of one individual.

To press this parallel more closely it may be pointed out again that sex is an example of genetically controlled dimorphism. But it is well known that in the domestic fowl, for example, castration followed by the implantation of a testis may cause a bird, which started life as a hen, to change the characters of its plumage and become a functioning cock. And in the duck simple castration causes the appearance of drake's plumage. Here we have a sort of metamorphosis, which serves to show how the action of the genes in development can be overriden or reversed by the action of hormones produced in the sexual glands. In a similar way it has been shown by Mme Charniaux-Cotton that the males of some Crustacea have an 'androgenic' or male-producing gland. If this is implanted into the female her sex is reversed and she becomes transformed into a male.

We are now in a position to consider a little more closely how the form of the insect and its metamorphosis are controlled. The only part of the insect which we normally see is the outer skin, or cuticle. The cuticle is the product of the single layer of cells, the epidermal cells, which form the surface of the animal. In the course of its development in the egg a structural pattern appears on the epidermis. In some regions it grows out to form legs or wings etc., in one area it will form soft and flexible cuticle, in other areas hard or darkly pigmented cuticle.

We do not know how the pattern or 'differentiation' of the different regions of the epidermis is brought about. But the interesting thing about the epidermis of the insect is that it contains not one pattern but two or three patterns: the larva, the pupa (if one exists) and the adult. It is true that in some insects certain groups of epidermal cells are separated from the general epidermis of the larva and form little packets or 'buds', which do not take part in the formation of the cuticle during the larval stages, and first come into action when they grow outwards and form the wings in the pupa and adult insect. But that is exceptional. In most insects the same cells (or their descendents) are responsible for producing in turn the larval pattern, the pupal pattern and the adult pattern. Each cell contains within it the machinery (the genetic machinery and the chemical catalysts, or enzymes, which the genes are believed to produce) that is needed to form the cuticle appropriate for its allotted element of the general pattern. And it can form this cuticle in three alternative types: larval, pupal and adult.

Moulting

What controls the appearance of these different forms? Before answering this question we must consider how the insect grows. The cuticle can stretch to some extent but it

Young cricket of the species Pachytylus migratorius: *the wings have not yet reached their normal shape or size. The cricket belongs to the group of insects showing incomplete metamorphosis, as we have seen at the beginning of this chapter (×3).*

cannot grow. In order that the insect may grow it must shed its cuticle, or 'moult', from time to time—after having first laid down a new and larger cuticle beneath it. True growth in the insect, therefore, takes place in a series of moults, and it follows that, whenever there is a change in the form of the insect during its growth, it happens abruptly at the time of moulting. In order to understand the nature of metamorphosis we must therefore know something about the moulting process.

As was first proved by the Polish biologist Stepan Kopeć forty years ago, the renewed growth which leads to moulting is brought about by a secretion from the brain. It is now known that the brain contains modified nerve cells (neuro-secretory cells). These curious cells produce a hormone which activates a gland of internal secretion in the thorax (the 'prothoracic gland') and it is this gland which then secretes the 'moulting hormone'. As a result of nearly ten years research the German chemists Butenandt and Karlson have obtained this hormone in crystalline form. It is named 'ecdysone' from ecdysis, which is the technical term for moulting. In one experiment, after starting with 500 kg of silkworm chrysalides they obtained 25 milligrams of the crystalline hormone. Its chemical nature is not yet known.

The moulting hormone, ecdysone, causes the epidermal cells to grow and divide and then to carry out the elaborate series of chemical activities which are involved in the secretion of a new cuticle. When this is complete, the remnants of the old cuticle are cast off, the insect expands its new cuticle by swallowing quantities of air and finally, by means of further chemical changes the new cuticle is hardened and darkened.

The problem now is what controls the type of cuticle that is laid down during this moulting process? In other words, what controls metamorphosis? The answer was found during a study of the South American blood-sucking bug *Rhodnius prolixus*. This insect, which is almost two and a half centimetres long when fully grown, has five larval stages which are more or less alike, but when the fifth stage moults it undergoes a striking metamorphosis: genital organs and wings appear and the whole structure and pattern of the cuticle is changed.

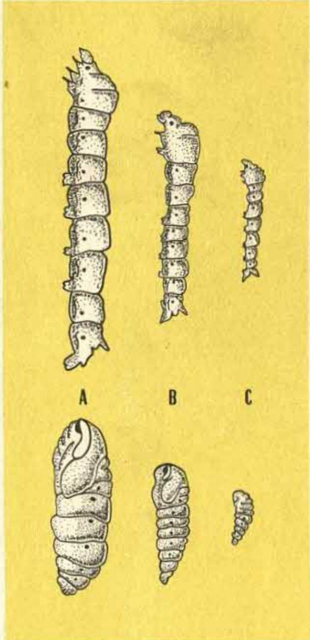
Rhodnius takes only one meal of blood during each larval stage—a very large meal which may be as much as twelve times its own weight. If its head is cut off soon after this meal the larva will not grow or moult, because the brain with its neurosecretory cells has been removed. But these headless insects will live for a very long time, slowly digesting their meal of blood. Indeed, we have had some which have lived for more than a year, which is longer than they would have lived if they had been allowed to keep their heads.

However, if the decapitation of a young larval bug is delayed until there is sufficient moulting hormone in its body fluids for it to complete its growth, a very surprising thing happens. Instead of turning into another larva when it moults, it undergoes a precocious metamorphosis and turns into a diminutive adult. Further experiments confirmed the suspicion that there is a second hormone secreted in the head, which normally prevents the young insect from undergoing metamorphosis.

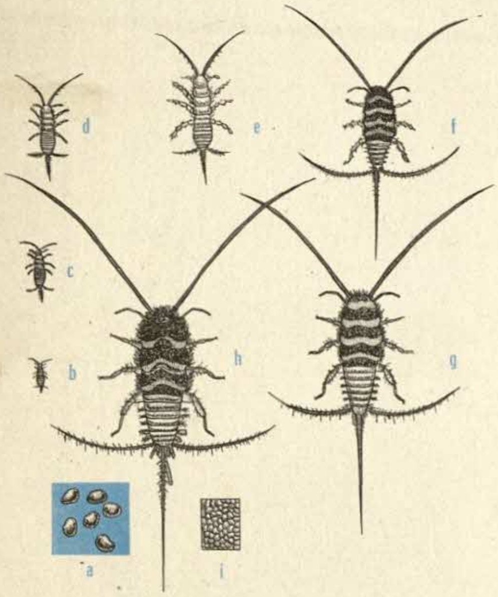
The juvenile hormone

The source of this hormone was soon located in a small gland of internal secretion lying just behind the brain, named the *corpus allatum*. The hormone itself is known as the 'juvenile hormone' because, so long as it is present in the body fluids, the growing insect retains its larval or juvenile characters. In *Rhodnius* the juvenile hormone is normally produced during each of the first four larval stages. In the fifth stage the hormone is no longer secreted and therefore, when the insect moults, it undergoes metamorphosis.

If a very small larva, recently hatched from the egg, is decapitated and caused to moult by joining it onto the tip of the head of a moulting fifth-stage larva, so that it is perfused with body fluids containing moulting hormone but not juvenile hormone, it will turn directly into a tiny adult bug. Conversely, if the corpus allatum from a young bug in the third or fourth stage is implanted



Results of the removal of the corpus allatum *on the metamorphosis of bombyx (the silkworm): (A) normally developed caterpillar and chrysalis, (B) caterpillar at fourth stage and chrysalis into which it has metamorphosed after removing* corpus allatum, *(C) caterpillar at the third stage and chrysalis formed after the same operation.*



The shape of Thermobia domestica *(silverfish) remains constant from the beginning to the end of its life. This insect shows no metamorphosis whatever.*

into the abdomen of a fifth-stage larva, so that this is now provided with juvenile hormone, then, instead of turning into an adult when it moults, it retains its larval characters and turns into a giant or sixth-stage larva. And on repeating the experiment it will grow into a seventh-stage larva.

Metamorphosis is brought about in the same way in all insects: cockroaches, stick insects, locusts, termites, bees, beetles and butterflies. To quote a single example, M. Bounhiol, of the University of Bordeaux. showed that if the corpus allatum is removed from a very young silkworm it will turn into a tiny chrysalis from which a tiny moth emerges.

It is interesting to note that, when the corpus allatum is removed from a young caterpillar, this does not develop immediately into an adult moth but it turns first into a pupa. This is sometimes regarded as evidence that the pupa is really a sort of first adult stage and pupation represents the time of metamorphosis. But it is possible to devise experiments which lead to the partial omission of the pupal stage so that the caterpillar turns directly into a monster intermediate in character between pupa and adult. Indeed there is evidence that the larva is developed when the epidermis is exposed to moulting hormone together with a large amount of juvenile hormone, the pupa is developed in the presence of moulting hormone plus a very little of juvenile hormone, and the adult under the action of moulting hormone alone.

By transplanting the corpus allatum from one kind of insect to another it has been proved that the hormone is the same (or at least has the same effect) in all. Many attempts were made to prepare active extracts of the juvenile hormone from insects, but for long these were unsuccessful. It seems that in most insects only minute traces of the hormone are present in the body at any given moment. But in the year 1961 Dr Carroll Williams, of Harvard University, made the interesting discovery that in the abdomen of the giant silkmoth, the *Hyalophora cecropia* moth of North America, there is a remarkable accumulation of juvenile hormone. All that is necessary is to extract the fats with ether and we obtain a bright yellow oil rich in juvenile hormone which produces just the same effects as implantation of a living corpus allatum.

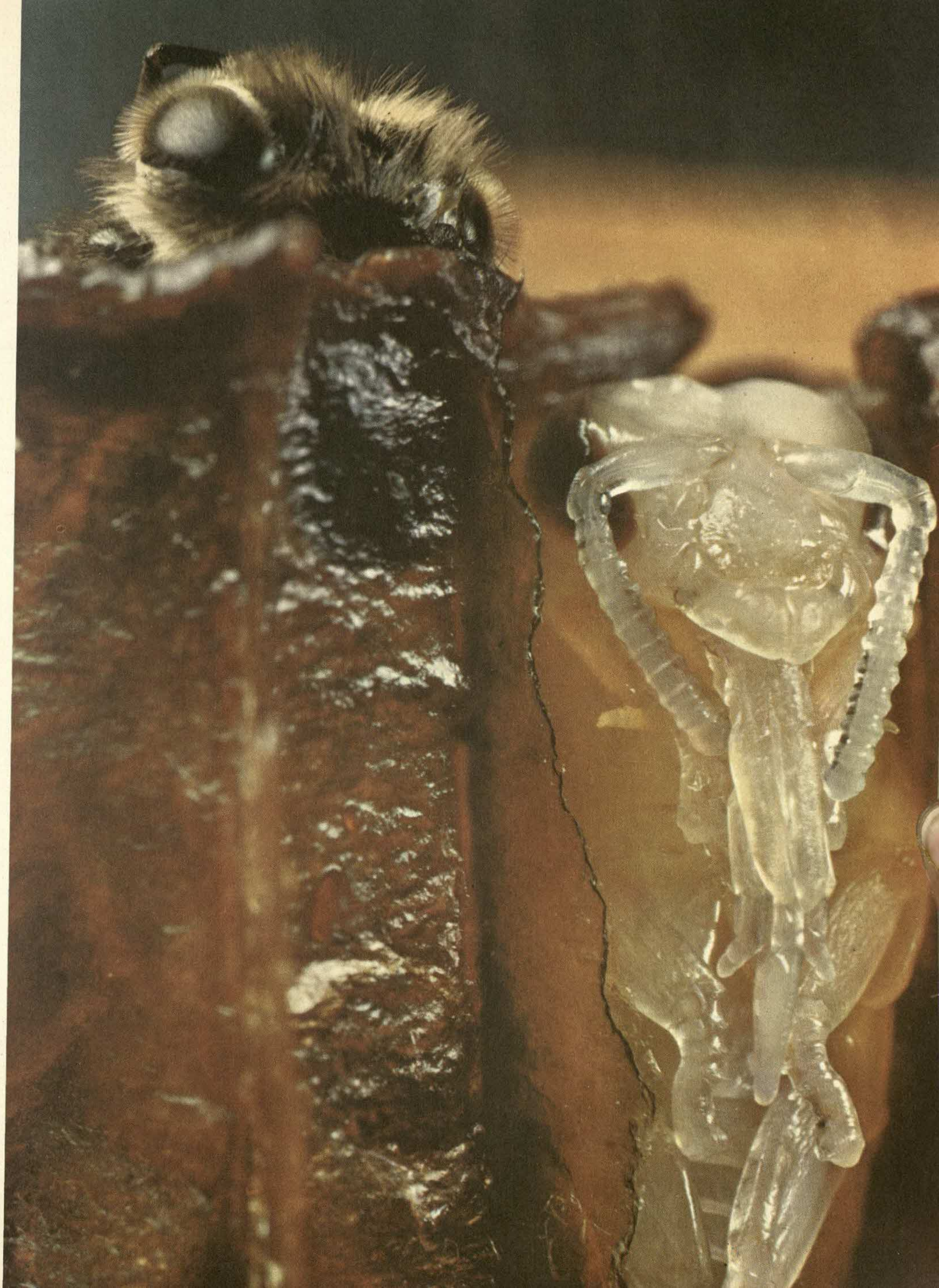
In some of the early implantation experiments it was not uncommon to obtain a perfectly normal adult *Rhodnius* which had just a little patch of larval cuticle immediately over the implanted gland. That proved that the juvenile hormone acts directly upon the epidermal cells, causing them to lay down cuticle of larval type. The same results could be obtained very easily with the active extracts containing juvenile hormone. It is only necessary to abrade the surface of the cuticle of a fifth-stage larva of *Rhodnius* over some restricted area and then to apply the oily extract to the outside in order to obtain, for example, an adult *Rhodnius* with one larval wing, with one larval segment interposed in the abdomen, or even with letters engraved in larval cuticle upon the surface.

Once these active extracts had been prepared, it became possible to devise methods for detecting very small amounts of the juvenile hormone and also for concentrating it, with the object of isolating it and discovering its chemical constitution.

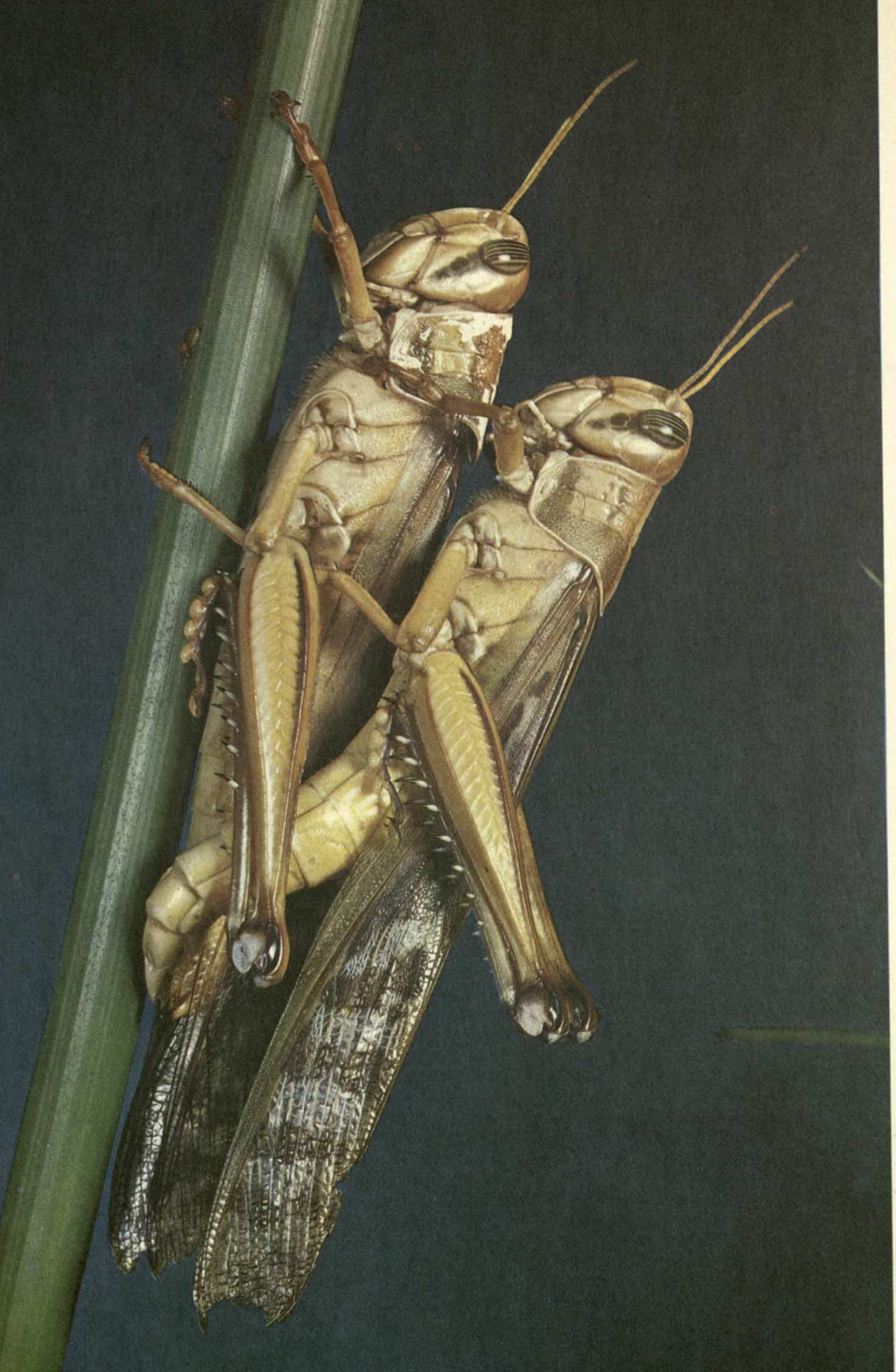
It has been possible to show that there are small amounts of juvenile hormone in extracts from all insects. But it has been discovered by Dr Williams and his colleagues and by Drs Howard A. Schneiderman and Laurence I. Gilbert that the juvenile hormone, or some substance with the same properties, is present, not only in many invertebrate animals besides insects, but in the suprarenal gland of cattle and in many other organs of other mammals and of man. It is even present in some bacteria. Whether it has any physiological function in these animals and plants is not known.

Quite recently a German chemist, Dr Peter Schmialek, working in West Berlin, has found that this widespread material with juvenile hormone activity is a mixture of the well-known substances farnesol and farnesal. It is highly probable that the insect has learned to make use of these substances and that the natural juvenile hormone is either farnesal or some closely related compound.

A word of caution is necessary about the name juvenile hormone. This name is apt to suggest that the hormone is a kind of elixir of youth which will permanently prevent ageing. But the male *Cecropia* moth contains plenty of juvenile hormone and yet it grows old and dies. In fact all that the juvenile hormone does is to control the development of characters that are already latent with the epidermal cells. It presumably acts upon the genes or the enzymes in the cell and favours the activity of those which are responsible for the development of larval characters. It thus merely controls the form of the insect; the problem of the ageing of the body is, unfortunately, something quite different.



The bee, a typical representative of the Hymenoptera, shows complete metamorphosis from the larval through the pupal to the adult form. Here, side by side, are a pupa, still unpigmented, curled up inside the pupal case, and a bee, fully developed, about to leave its case. (Mag. × 20. Photo Lod).



*Copulation in the nomadic locust (*Nomadacris septemfasciata*, East Africa, Tanganyika). The abdomen of the male makes a twist to join up with that of the female. (With thanks to F. O. Albrecht, in charge of research at the Laboratoire d'Evolution des Etres Organisés, Paris. Mag. × 3·5. Photo Lod).*

Animal sexuality

Jacques LECOMTE

> *In its most primitive form love is directly connected with the taking of food. It is in some way a hunger of the whole organism directed towards a similar one which, however, not being quite the same, offers the mysterious attraction of the stranger. This affinity of the one for the other, this desire for another, will finish either by a complete and final fusion of the two subjects or by a passing union after which they will separate again, both a little different from what they were before.*
>
> JEAN ROSTAND

Everything happens as if nature were preoccupied with creating more and more lives.

The basis of the phenomena of reproduction is to be found in sexual differentiation. In spite of numerous exceptions, in spite of the particular case of asexual reproduction, it is the union of two partners of different make-up which remains the chief law of nature. Even among the unicellular animals, side by side with asexual reproduction one finds numerous examples of conjugation in which the cell material of two individuals is exchanged as in the slipper-animalcule *Paramecium.*

We do not intend here to describe the complicated cycles and curious combinations which one finds among the Protista or single-celled animals. Suffice it to say that sometimes the two cells which unite are very different one from the other, a state known as anisogamy, whilst in other cases the cells appear very similar or isogamous.

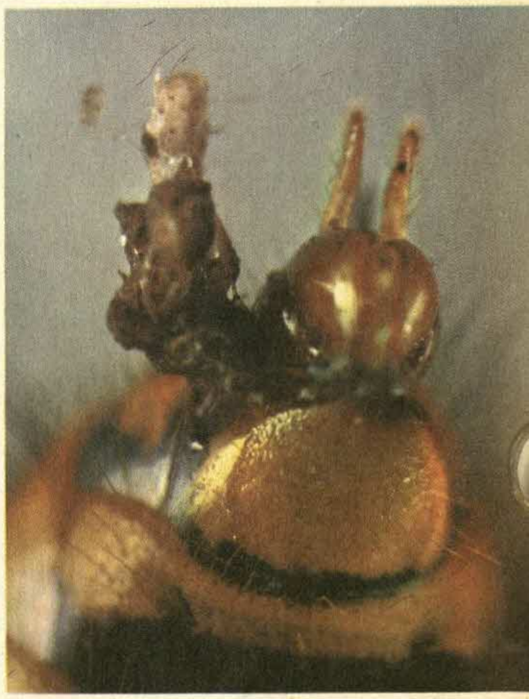
A classic example of anisogamy is found in the parasite which causes malaria, the *Plasmodium.* Among the isogamic types we may include the Foraminifera, but even here there is only the appearance of isogamy, since it has been shown that the similarity between the two partners is only superficial and their internal physiological differences really profound. For example, they do not stain in the same way with vital dyes, which shows that they have a different chemical constitution.

Sexual dimorphism

When we turn to multicellular organisms, we find that here the differences are even more striking and these differences constitute what is known as sexual dimorphism.

This dimorphism can show itself in the most varied ways. Sometimes it is a question of body size, as in the mammals where the male is larger and stronger than the female, whilst among the batrachians such as frogs and toads the opposite is the rule. In birds there is no general rule, the male being sometimes stronger and larger and in other cases smaller than the female. Amongst insects, too, there is much variation. Thus the queen termite dwarfs the puny male by its size, while among the Coleoptera, like the stag beetle or the Hercules beetle, the males are very much stronger and better developed than their females. In the spiders the male is usually smaller and often a mere dwarf compared to the female. Nevertheless in all these cases we are dealing with normal animals, possessing all the characteristics of the species. There are yet other instances in which the reduction in size of the male is accompanied by so profound a change that the animal may be regarded as a parasite.

The best-known example of this is a marine worm called *Bonellia* in which the female has the appearance of a greenish ball a few centimetres in diameter which is prolonged into a sort of trunk twenty or thirty centimetres long. Within this trunk we find microscopic animals which are, in fact, the males living in the interior of the huge female as if they were parasites. There are many other examples of degenerate males, but only one other will be mentioned here which was



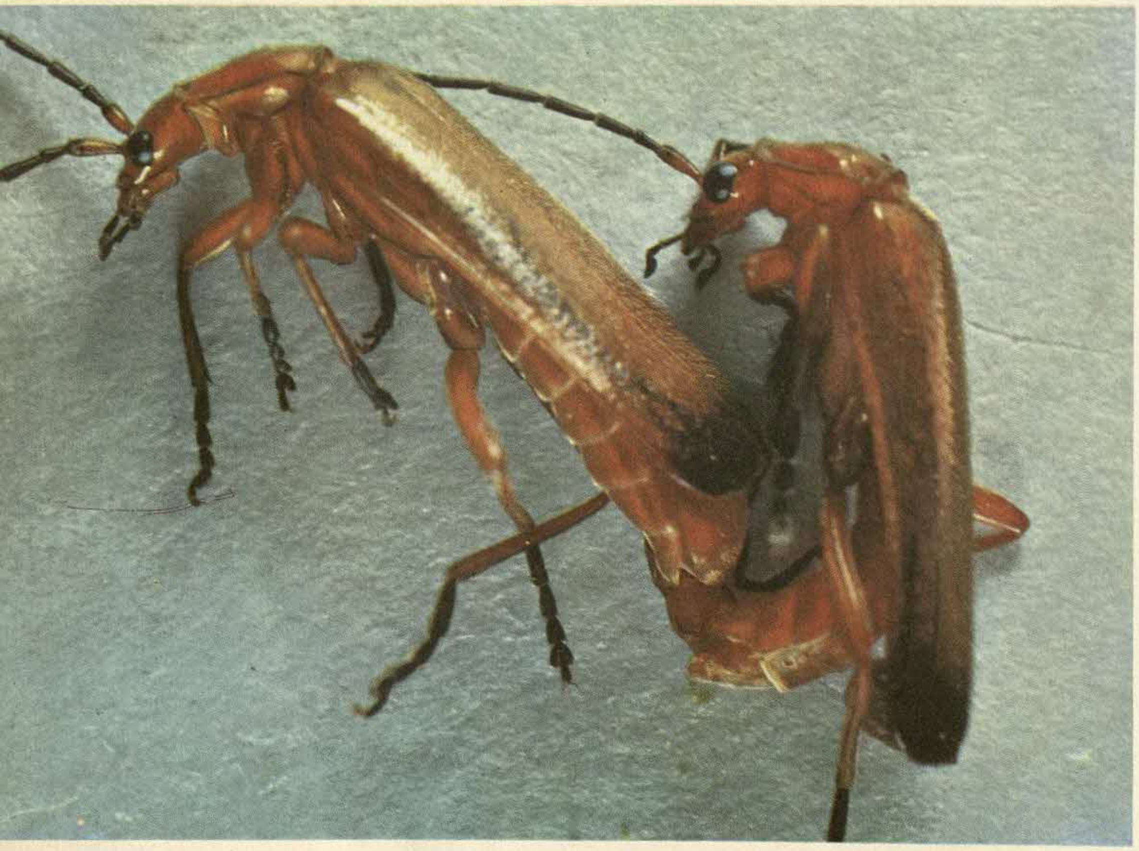
When the queen bee has been fertilised she pulls away violently from the male, tearing off his genital organs. The photograph shows the abdomen of the queen with the male organs attached. (Mag. × 15, Photo Lod).

discovered by C. Tate Regan and is all the more extraordinary since it occurs in a vertebrate. It concerns Ceratioid deep-sea fish, the females of which carry males imbedded in the skin of their abdomen. These are truly parasitic since they live grafted on to the blood circulation of the female.

Another feature apart from size is the variety in colour between the sexes of a species, and it is amongst the birds that we meet the most beautiful examples of sexual colouration. From the barnyard cock and the drake to the most brilliant of the birds of paradise, the males rival each other in beauty, in singular contrast to their modest females. There are also numerous species of fish which, either permanently (as in the fighting fish) or during the mating season (as in the stickleback) demonstrate special adornments confined exclusively to the males; the same is true of some of the batrachians, for example the newts.

Besides size and colour a multitude of other characteristics can indicate sexual differentiation. We will mention just a few here: the antlers of stags, the mane of the lion and the beard of man, among the mammals; and among the invertebrates we find similar examples such as the pincers of the stag-beetle and the sea-spider, or the combs on the anterior legs of *Drosophila*. Sometimes the differentiation affects the sense organs, and again it is usually the males which have the advantage. In this category are the antennae of moths and the eyes of drone bees or the male mayfly.

Among insects the process of copulation often takes a very complicated form and may sometimes last for days. In some cases it ends with the death of one of the partners. (Photo Lod).



Circumstances of differentiation

We have given enough instances of differentiation, the sum total of which would fill volumes, so it is now time to ask some questions. Two come at once to mind. How, and why, does sexual dimorphism occur?

It is relatively easy to answer the first question.[1] These differences, which are known collectively as secondary sexual characters,[2] have in most cases a known cause and in the case of the vertebrates there is plenty of evidence pointing to the role played by the hormones produced by the sex glands, the ovary and the testis. Sometimes hormones from other glands play an important part, as in the nuptial plumage of certain birds which is under the influence of the hormones produced by the pituitary gland at the base of the brain rather than those of the testis. In the case of the invertebrates the origin of sexual dimorphism unfortunately remains for the most part unknown.

So far as the second question is concerned, the why of secondary sexual characters, the most obvious approach is to consider the actual sexual behaviour of animals. A few typical instances will be more enlightening than lengthy generalisations.

A curious example is found among the bower birds. These birds, which are close relatives of the birds of paradise, live in Australia and New Guinea where they are quite common. During the breeding season the males adopt a very interesting behaviour-pattern in order to attract the females. They build a sort of little house in a clearing, the shape and size depending on the species, and ornament it in various ways. In front of the door of this building they make a garden from which all growing vegetation has been carefully removed and proceed to decorate it with picked flowers, shells, bright stones, and all sorts of unexpected objects which may be found in the neighbourhood, such as old cartridge cases, mutton bones and so on. The male bird remains permanently in attendance and walks about, apparently demonstrating the most beautiful pieces in his collection by moving them around from one place to another. This stratagem unerringly attracts any females in

(1) *In some groups of insects (Diptera) and in mammals the determination of sex is genetic and effected at fertilization. It depends on a balance between male-modifying genes and female-modifying genes carried in the chromosomes, of which there are two X-chromosomes in the female and one X- and one Y-chromosome in the male. In other insects (Lepidoptera) and in birds the situation as regards the sexes is reversed.*

the neighbourhood and one of them will eventually join the owner of the most decorative bower. In this case there is no pursuit of the female but rather a process of attraction.

Sometimes it is the female which attempts to attract the male, but this is usually by some less active stimulus. It may be the release of an odorous substance (as in the female moths) or of a light signal. This last method has not yet been fully studied but everybody is familiar with the glow-worm. There is also an American insect, *Photinus pyralis*, which has developed a quite elaborate system of signals. The males of this species send out a beam every six seconds as they fly to and fro, whilst the females who are attracted in this way respond from the ground by emitting a beam precisely two seconds after that of the male.

Some marine worms have similar habits and here the female has a particularly active role, since she swims on the surface of the water in small circles, sending out an intense light. This circle of light forms a signal for the *Odontosyllis* males which are lying on the sea bed and rapidly rise to the surface.

Seduction and reconnoitring

In fact the techniques of seduction show an infinite variety. One of the most striking is the offering by the male to the female of a gift which she desires. In certain dipterous insects (i.e., those with one pair of wings) known as the Empidae, the male brings a small insect which he offers to the female. The prey may be eaten by the two partners before copulation, or by the female alone during copulation. It sometimes happens that the prey is not in fact eaten at all, acting merely as a stimulus. In other insects the prey is surrounded with a ball of silk or saliva, or the ball may contain nothing edible, but a flower petal, or it may even be empty. In these cases the female goes through the motions of chewing this symbolic offering and copulation then becomes possible. Afterwards this offering is left lying on the ground, and may be used again by another male who, in turn, will leave it behind. Such offerings of food or other gifts are not infrequent; many instances are known, particularly among birds, to say nothing of man.

Do these facts, interesting as they are, really elucidate the part played by the secondary sexual characters? The answer is yes. Detailed study of these and other examples shows that this type of behaviour is designed either to show off the distinctive sexual characters, or to prolong their effect and if necessary to supplement it.

Two Daphnia. *These water fleas, which belong to the group of lower crustaceans, are remarkable for their mode of reproduction by parthenogenesis. The females lay eggs which develop without fertilisation and give rise only to other females. (Mag. × 150. Photo Lod).*

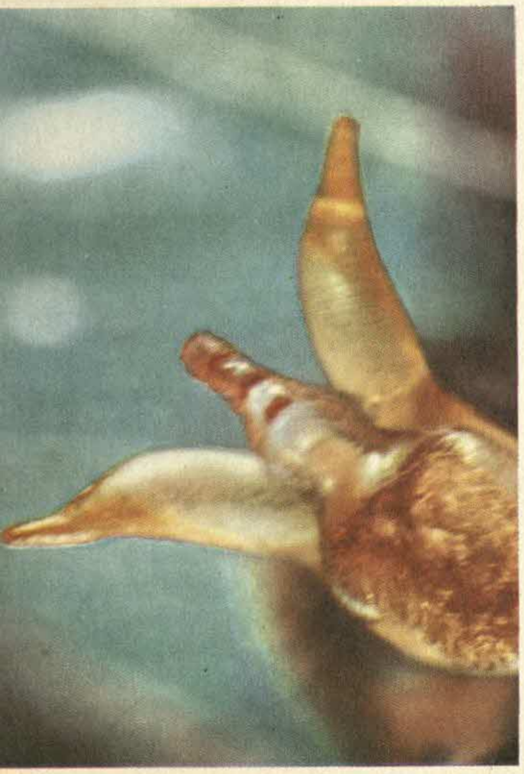
Usually an animal of one sex can readily recognise the sex of another member of the same species, but on occasion this may be more difficult. Moreover, it is not enough for an individual to be recognised as belonging to a given sex; for a state of sexual receptivity must also be made apparent. Animals, with few exceptions, show sexual behaviour only during one season of the year, the mating season, so it is not surprising to find that in some species the characters which indicate sex are only apparent throughout this period. Besides, the female may be receptive only for a short time and signals to indicate this state are essential. The extraordinary habits of the bower birds and the flies of the Empidae family are only manifestations of secondary sexual characteristics, analogous to the morphological characteristics we have discussed earlier, and the same is true of all sexual displays. To sum up, all these characters play the part of signals, making clear not only the sex of the individual, but also the state of sexual receptivity.

Sexual union and fertilisation

We come now to another aspect of sexual behaviour, the actual union of the sexes and the process of fertilisation. There are two main

(2) *Secondary sexual characters are those, other than the reproductive glands and ducts, by which the sexes differ; they were given this name by John Hunter. When they play a part in behaviour resulting in sexual reproduction they are called epigamic characters (E. B. Poulton, Sir Julian Huxley) and include those to which Darwin attributed a role in sexual selection.*

EDUCATION



The sexual organs of insects show a great diversity of form and often have a curious structure. This picture shows the genital organs of the male honeybee, the drone, which has no sting and lives in the hive as a parasite, taking part only in the reproductive process.

types of fertilisation, internal and external. In the case of external fertilisation the ova and the spermatozoa are released into the immediate environment meeting each other independently of those who have produced them, and quite often there is no particular approach to each other by the male and female partners. This happens in animals which normally live in groups, like sea-urchins and many shellfish. All that is necessary is that the sexual cells of the two sexes shall be released more or less simultaneously. In other cases, there is some active behaviour, for instance the female may prepare a site for the eggs to be laid in and the male then comes to fertilise them. This type of behaviour is found quite widely among some fishes.

Some forms of sexual behaviour are intermediate between external and internal fertilisation. Their common characteristic is that the ova always remain in place inside the female, while the spermatozoa pass through a free stage before they reach the ova. This is the case with the small shellfish of the barnacle group whose shells encrust the rocks of our coasts, and also with larger species of shellfish. Although they are hermaphrodites carrying both male and female sex-cells they have to be fertilised by another individual and their reproduction bears some resemblance to that of the sea-urchin in that the sperms are liberated directly into the water. However, the ova remain inside the body and it is there that fertilisation takes place.

Among some rather primitive arthropods, the group containing the insects, spiders, and crustacea, a curious procedure employed is that of the spermatophore. This is a small capsule containing the sperm which is left by the male at the top of a long stalk, and if it is found by a female she uses the contents to fertilise herself. Thus the male and the female never meet. An even stranger example is that of the argonaut, a sort of cuttlefish in which the female has a hard shell; these animals do not meet each other either and their relationship is a very long-distance affair. In fact, one of the arms of the male, containing the semen, is cast off and swims away independently to seek the female which it will fertilise.

Finally there is the type of fertilisation which we call copulation, and this entails a union of the two partners for a longer or shorter period of time. Here again the methods are legion. The millipedes, profiting by their numerous limbs, use two pairs of legs to introduce their semen into the body of the female, and certain male lice, ignoring the normal genital passages, inject their spermatozoa directly into the body of the female leaving them to spread throughout it and finally reach the ova. Ticks have another pattern of sexual behaviour, the male introducing his beak (the organ normally used in feeding) into the genital orifice of the female and enlarging it before inserting spermatozoa.

Another species of the Hemiptera or sucking insects has habits which are even more cruel. During copulation the female thrusts her mouthparts into those of the male, and during the actual process of coitus sucks out all his internal organs so that at the end of the act all that remains of him is an empty shell. The same fate lies in store for the male praying mantis.

Even when we come to the use of a specialised external sexual organ, the variety of forms that this takes, and the method by which it is used, is considerable. Take, for example, the sex organ of the male honeybee (the drone). This apparatus is so complicated that its owner cannot extract it after copulation and has to leave a part in the vagina of the queen.

Among vertebrates the process is less varied. It is noteworthy, however, that snakes and lizards have a double penis, though they use only one at a time. Most birds have no similar organ at all, so that there is only contact between two cloacae (the common excretory and genital orifice) which nevertheless allows the transfer of sperm to take place.

The time taken for copulation is very variable. Among birds it may be as brief as a few seconds, whilst in the case of the mammals, that of the ferret may last as long as two hours, and some insects remain coupled for whole days at a time.

In short, the mechanisms of sexual union are infinite in number, but there is the same driving force behind all of them.

In the words of La Fontaine: 'Let all living things love and let all living things flourish, the monsters on the ocean bed, tigers in the forests, and larks in the fields'.

The study of extreme environments

Claude DELAMARE-DEBOUTTEVILLE

Living beings may be studied in their natural surroundings in one or other of two ways, of which the first and older method is to consider a plant or animal individually, as a single species. The observation of the habits and behaviour of each species is a fascinating pursuit, and this relatively old-fashioned 'natural history' remains, although some naturalists have abandoned field work in favour of the laboratory, where the harvest to be reaped is just as abundant and possibly is more easily added to by successive generations.

The second method is a more composite one which has been introduced much more recently. Animals and plants are not considered in isolation from each other, but as interacting units in a given environment; instead of looking at one particular plant, a survey is made of the complex pattern of the vegetation. The first man to apply his curiosity to the analysis of large groups taken as a whole was Alexander von Humboldt.[1] Botanists (or more particularly those who are plant sociologists) have made rapid progress in this field, whilst zoologists are relatively far behind because animals are so much more mobile and harder to get hold of. Botanists have shown not only that plant species are dependent to a varying degree on regional conditions, but also that there are statistical laws which apply to the pattern of vegetation in any particular region, and enable us to define its make-up with considerable accuracy. In other words, a plant community is not anarchical but organised; it is not the result of chance, but of history.

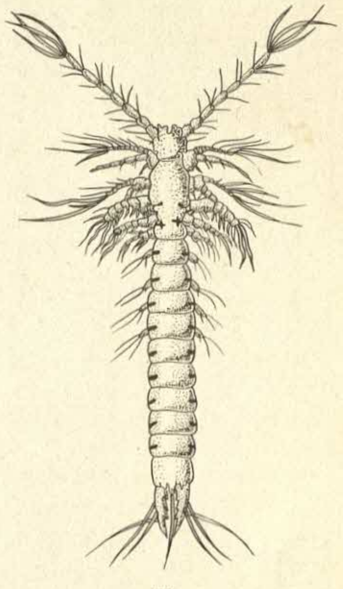
It is indisputable that the physiological characteristics of the species concerned play an important part in the colonisation of a region. We must not underestimate the decisive role played by the reproductive potential and the method of reproduction,[2] if the life-cycles are complicated,[3] nor the effect that climatic factors have on photosynthesis, or assimilation. But these specific factors are not the only ones that interfere with the regional equilibrium; for there are far more subtle links between the various species of plants. Thus the bacteria and fungi in the soil may help or hinder development and these minute organisms act directly on the population balance by working selectively on the anatagonisms between the species. At a more complex level, regulating mechanisms are found which to some extent resemble the phenomena observed in higher organisms.[4] In this way hormones may maintain a specific equilibrium within a plant and prevent another from establishing itself. Phytosociology is the study of these interspecific links and interactions in the vegetable world.

Amongst animals conditions are very different on account of the mobility which tends to obscure the many subtle links uniting one species with another. Nevertheless, if we look hard enough, we notice that each animal species is directly or indirectly linked to every other species living in the same environment. Thus the natural population of an area appears as the sum of many component populations of different species which are interacting with each other according to their own particular physiological, ecological and ethological characteristics.

Natural populations

When observing the fauna of an environment, it is not simply a matter of comparing these relationships with sociological phenomena in the strict sense of the word. Indeed, unlike botanists, zoologists include the study of true animal societies, such as are found among vertebrates, ants, and termites, and which are not strictly comparable to the population of a natural environment.[5]

So numerous are the publications on ecology brought out each year, that it is impossible to give any idea of all the recent developments. Nevertheless, by careful analysis, we are beginning to get a fairly objective idea of the way in which natural populations evolve. We know that as a rule the more extreme the conditions in an environment, the smaller will be the number of species that live in it and the greater the number of individual members of each of these species. Conversely, in natural populations under temperate conditions, the variety of species is more important than the numbers within each species.



A mystacocaridian crustacean, a real living fossil. Recently discovered, it lives in the interstices between the grains of sand on sea beaches.

---

(1) Alexander von Humboldt: *the celebrated German naturalist (1769-1859), author of* A Physical Description of the World *which sets out the results of his numerous voyages from the point of view of zoology and general biology.*

(2) Reproductive potential: *the maximum number of young which can be produced under optimal conditions.*

(3) Complex cycles: *refers to certain larval forms which, for example, have to pass through several different hosts before reaching maturity; or, on the other hand, they may have to change their environment or habits.*

The detailed interpretation of these fundamental laws of distribution presents considerable difficulties. It must not be forgotten that past events have often drastically interfered with the development of populations and imposed their particular pattern upon them. Consequently, within the framework of the regional economy, the possibility must be borne in mind of immigrations which may have taken place in the course of time and these cannot be analysed without the aid of a modern classification which is accurate both at the level of species and sub-species. In the conditions under which natural environments were formed they have all functioned in general like the 'empty spaces' described by Cuénot.[6] They have been populated by species already living on their frontiers which were both morphologically and physiologically highly adapted to the environment. If their specific make-up proved to be compatible with the conditions of their new home in at least one part of their range of variability,[7] these species have been able to build up large populations. Ecological selection has acted to eliminate incompatible variations and the new bonds established between the different species in the new environment have, in some cases, enabled new mutations which were previously disadvantageous, to be preserved. It is by such a process that one can explain the differentiation and rapid evolution of new species or genera, depending upon the environment to be colonised, in the great geocratic[8] periods of the geological past.

It is equally important when analysing species penetrating new environments to take into account from the beginning their ability to become indigenous. It is noticeable that, under present-day conditions, populations are more independent of one another than might be expected at first sight. For, if the continuous intermingling that takes place between one continent and another by way of the aerial plankton[9] is taken into account, as well as everything which drifts over wide areas in the seas, the populations of the different continents might be expected to be less individualised than they actually are.

In reality such natural populations are so well adapted and organised that each functions as a harmonious whole, resisting new colonisations. Strictly speaking, all the niches are occupied and there is no room for new arrivals. However, should a new species find an unoccupied place, or be able to supplant one of the occupants because of its particular physiology, then its colonisation will be extremely rapid and will profoundly change and upset the equilibria in the originally well-balanced fauna. For examples of this type of colonisation it is only necessary to consider the introduction of rabbits to Australia and goats to the island of St Helena.

Extreme environments

It is sometimes a thankless task observing living things in the fields, meadows or clearings since our imagination is not always sufficiently stimulated by what we see. Nothing is harder than to analyse the everyday world in which we and those close to us live. Our imagination is caught more easily by problematical things, rare combinations and exceptional manifestations. This is why many ecologists, little interested by the study of the soil we live on and derive our existence from, have shown greater interest in the study of extreme environments where life exists only in the face of severe limiting conditions.

Surprising though it may seem at first sight, this way of working is perfectly legitimate from the scientific standpoint; it is, in fact, an application to the living world of the principle of limits. Experience of extreme environments is able to furnish us with original data enabling us to have a clearer understanding of what life is and how it survives and maintains itself under so-called 'normal' conditions.

Moreover, if we consider what we mean by 'normal' conditions it is obvious that they are only thought of as such in terms of our own ideas as to what constitutes 'comfort' for human ecology. Twenty degrees centigrade is what we call a normal temperature, but twenty degrees above the freezing point of water has no special significance in the life of an animal belonging to a group living solely in dry, hot deserts. Such a norm has little meaning when we are considering the events of life in detail and is simply of value for reference or comparison.

When we look at the distribution of living things in nature today to discover the causes of the balances existing between them, or why some species have expanded their range while others have become restricted, we must realise we are exactly in the position of a man looking at a snapshot. The forms at any one instant are accurately portrayed, but the movement is stopped, so that a ball is arrested in mid-air, legs in a leap, or arms in a dive, and if it were not for our system of complex references arising from experience and aided by our memory and imagination, the movement of the ball, dive or leap, would not be impressed

---

(4) *It is thus that plant hormones are responsible for the maintenance of many specific equilibria and prevent others from becoming established. It is because of these mutual attractions and interspecific links that the study of plant communities has taken the name of phytosociology.*

(5) *If the zoologist studies one species in its environment and tries to understand why this species is adapted to its specific conditions of life as a function of certain physiological mechanisms, he is concerned with ecology in the strict sense, or* population ecology. *If, on the contrary, he is particularly concerned with analysing the total population of a certain environment in order to understand how the various species interact with one another, he is concerned with* community ecology. *On the other hand, he may take one particular species in its environment and try to understand its behaviour and the impulses which direct it, and in this case he is an* ethologist. *The close relationship between population ecology, community ecology and ethology is clear, since the study of the population ecology of an area cannot be undertaken without considering also its community ecology and ethology. Likewise, ethology undertaken without realising its ecological basis would be both futile and intellectually unsatisfying.*

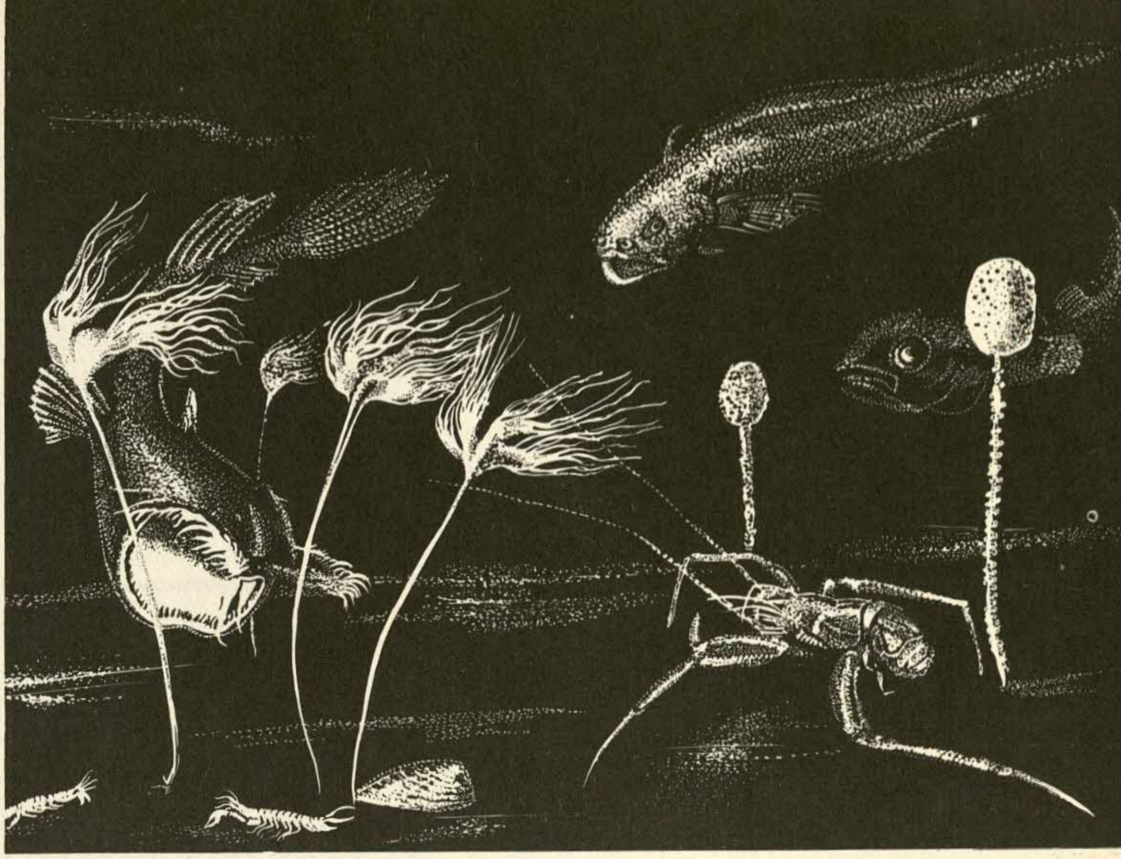
(6) L. Cuénot: *a contemporary biologist known for his works on genetics and evolution. Cuénot has been largely responsible for developing the concept of the 'empty space' discussed here by Delamare: a piece of ground newly emerged from water (for example, after prolonged flooding which has cleared it of its population) forms an 'empty space' without a fauna of its own, which will nevertheless soon be colonised.*

(7) Range of variation: *possibilities for variation of shape or function the extent of which depends on hereditary factors.*

upon our minds. For the biologist, nature is living in the sense that the component units, that is the species and individuals, are endowed with movement. But, looked at in a wider perspective, they are only the momentary and current forms of thousands of movements and specific events which have taken place over the ages. As with the snapshot, we would not be able to reconstruct these movements without the use of systematic cross-checking and the flair for discovery which form the complex references and rewards of the biologist's work. Therefore, if we are to incorporate all living phenomena within a common framework, it is perfectly legitimate to describe the most unusual and unexpected of them; those which have been able to carry life to the limits of its resistance on this planet. To study life is also to discover its resourcefulness.

The theory of panspermy

The problem of the origin of life on Earth has always been profoundly interesting to scientific minds, although modern work tends to present it as a primarily philosophical question of frontiers and boundaries. Some scientists have sought to explain the origin of life on our planet by visualising the ecological conditions obtaining on the Earth when it was much younger and taking into account what is known of bacteria, viruses, and proteins. Others have preferred to make the problem an even more remote one, so distant that it can hardly be analysed, by supposing that life had its origin on other planets; for they believe that the first seeds of life reached us by falling from the sky after traversing the interstellar spaces. This theory of 'panspermy' has only one advantage, perhaps a moral one, in that it does away with the scruples we may feel about living on a planet uniquely privileged among all those in the universe, a belief which is highly unlikely on the grounds of probability.



At great depths the specialised conditions of life produce some bizarre forms. Antennae and whiskers of inordinate length, enlarged sense organs and lighting devices. (After T. Wolff).

But is it possible to determine whether or not life was able to withstand journeying through the empty distances of interstellar space? Naturally, it is only possible to experiment on existing forms of life, all of which are the specialised result of a very long period of terrestrial existence and the experiments themselves lose a little of their scientific and philosophic validity on this score. However, here are some data about existing forms of life: certain seeds are still able to germinate after a long period in liquid air at − 172°C; dehydrated pollen, bacterial spores and fungi can survive at a temperature near absolute zero for quite a long time; and some tardigrades, little animals which can be 'brought to life' from a death-like state, can be revived after heating to 150°C. So it is not impossible to imagine that rudimentary forms of life, analagous to the viruses, could have resisted the cold of interstellar space and the tremendous heat resulting from their re-entry into our atmosphere. But at once new problems are created as to how these seeds of life could have left another planet, travelled through space, and arrived here.

We must let the problem rest at this point. Whether life originated on Earth or elsewhere, it showed itself at first to be capable of conquering its environment, being more contagious than the most responsive mother liquor to seeding with a crystal, and more dynamic than the most successful machines. Whilst it is not impossible that the events leading to the origin of life could still take place today (for how can we be sure that viruses do not originate in the depths of the oceans, when there remains so much that we do not know about viruses which have certainly existed for millions of years?) it is nevertheless a fact that organisms seem to be extraordinarily well-adapted to the conditions in the environments they have already conquered.

(8) Geocratic periods: *periods in which new forms, such as the mammals, make their appearance.*

(9) Aerial plankton: *all the minute invertebrates, such as insects, which move about in large numbers in the atmosphere within a range of 5,000–6,000 ft.*

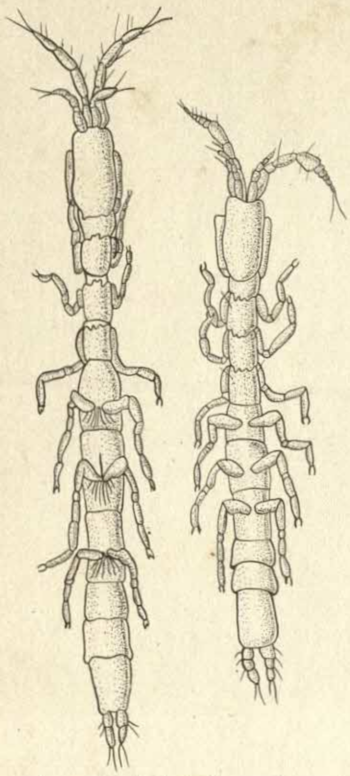
(10) Abyssal regions: *oceanic trenches with a depth which may exceed six miles.*

(11) *It should be noted that the presence of living bacteria in these oil deposits has been taken as evidence of a biological origin of the hydrocarbons which make up the oil. The study of sulphur deposits seems to show that the sulphur-reducing organisms appeared comparatively late in evolution (less than 800 million years ago).*

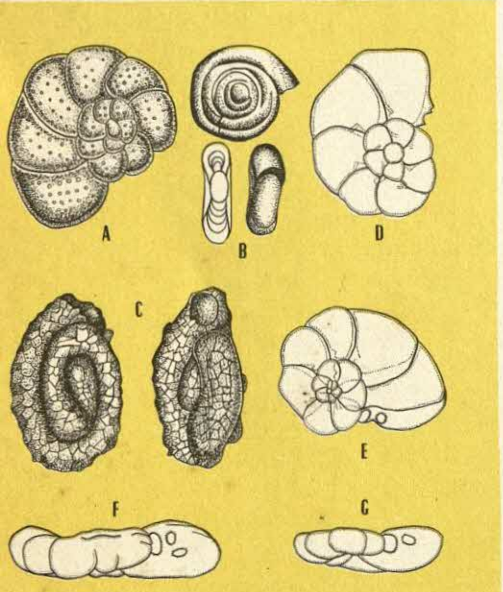
(12) Benthic: *the population of deep waters as compared with the plankton on the surface.*

(13) Biocoenosis: *a term applied to organisms which invariably live close together in the same environment.*

(14) Stereotropism: *the tendency to hide in the interstices of rocks and sand or in small spaces.*



Two small isopod crustaceans (Microcerberus monodi *and* M. machadoi) which live in *the interstices of the grains of sand on sea beaches.*



Foraminifera from deep subterranean stretches of land-locked water. During the course of their long isolation they have not evolved much, remaining similar to their marine relatives.

Conditions of life in extreme environments

It seems logical to continue this account by giving some indication of the knowledge acquired in the vast world of the bacteria. It is known that bacteria possess remarkable biological resistance, since various species can live equally well in the presence of oxygen (aerobically) as in its absence (anaerobically). They are little affected by high pressures and in all environments and under all conditions play a predominant part in biosynthetic activities. There are also other environments in which the bacteria appear to exist under even more extreme conditions, in particular in the great oceanic depths and in petroleum deposits.

The microflora of mud from the deepest parts of the ocean is rich in bacteria, and species have been brought up from at least 33,000 feet which flourish at the enormous pressures existing in the abyssal regions[10] to which they have become adapted. Fairly detailed studies have been made by the American bacteriologist Zobell which showed that, out of sixty-three species of surface bacteria cultured, only one-tenth are able to survive if they are exposed to a pressure of 600 atmospheres (the pressure at a depth of 20,000 feet). On the other hand, the species normally living in the abyssal regions, called for this reason 'barophilous' (pressure loving) are closely adapted to the pressure existing in their natural environment; for the best conditions under which to grow and culture them is at 1,000 atmospheres and a near-zero temperature. The characteristics of these species are surprising enough at first sight, yet the biochemical properties of the cell walls must be very remarkable to enable them to remain in equilibrium with their environment under such extreme conditions, and their characteristic enzymes must be equally unusual to function under such very specialised circumstances.

When the oil men carried out elaborate researches on oil-bearing strata they were able to show that the water gushing from oil wells contained numerous living sulphur-reducing bacteria. Many authors immediately reported the presence of *Desulfovibrio desulfuricans* in association with non-pigmented aerobic bacteria (*Thiobacillus*) and red sulphur bacteria (*Rhodothiobacteria*) in the deposits of the U.S.A. and the U.S.S.R., at depths of between 400 and 6,500 ft. These bacteria are undoubtedly native to the oil-impregnated rocks and in this situation prove to be resistant to extreme temperatures of 75°C to 95°C. Here it might be said that we are really confronted by a kind of subfossil life, represented by those organisms which have lived under extreme biological conditions from very early times.[11]

Leaving the realm of bacteriology which, of course, is a relatively specialised study, we must now consider a number of environments which are interesting from the point of view of their natural equilibria. In reality many environments, normal for some of their inhabitants, are highly specialised for others, since biological eccentricity is strictly a function of individual venture.

Although remarkable adaptions to marine life exist, their environment should be regarded, not so much as an extreme one, as one which is vast and widespread. However, it may be pointed out that numerous organisms described as benthic,[12] which live in the depths of the ocean correspond to the different surroundings and different types of sediment in a quite remarkable way. These benthic groupings, other things being equal, are so constant in their statistical composition, that some have regarded them as communities endowed with multiple interactions and self-regulating processes which give them the impression of genuine superorganisms living in a state of biocoenosis.[13]

While the existence of biocoenoses on the land-masses is indisputable, those in the sea occur on an infinitely larger scale. Within the sandy sediments, between the grains of sand, live millions of strange little animals and this interstitial environment is clearly very different from the whole of the surrounding marine ones, so extensively have the species which populate them been modified by their special way of life. So the researches of recent years by such workers as Delamare, Remane, Schultz, Swedmark and Teissier, have revealed a new world in which there live such species as the extraordinary medusa *Halammohydra*, the equally odd primitive crustaceans or Mystocaridae, and many other types each more bizarre than the next. All these are severely moulded by their environment, being small in size, unpigmented, blind, armed with adhesive organs, endowed with an active stereotropism[14] and largely insensitive to alterations in temperature. Characteristic, too, are their curious modes of reproduction. They lay only a few large-sized eggs, rich in yolk reserves, and embryonic development is prolonged at the expense of post-embryonic development. This development tends to be direct, the pelagic larvae[15] being more or less completely suppressed. In this way the environment functions effectively as a closed world, completely isolated from neighbouring marine environments, but even though this is extreme, all the lines populating it are to be found in the open seas.

It is from this very diverse and specialised interstitial world that the population of the sediments of the littoral and continental shelves has been developed throughout the ages and is still being developed today. Detailed analysis does not reveal any essential differences between the populations of different sediments: it is simply that the population of the continental sediments appears to be infinitely poorer in quality and quantity. The species in the deep continental waters have sometimes been shut off from the rest of nature for very long periods, yet belong to lines which still live in the marine interstitial environment, and it is no exaggeration to say that in the sedimentary masses of the depths the life of the ancient sea-shores continues to perpetuate itself.[16]

In hot springs life has become much more diversified than one might expect. Red and green thermophilous algae which live at more than 70°C have been known for a long time in the springs of Karlovy-Vary (Carlsbad) in Czechoslovakia. However, these organisms have evolved little and their appearance is relatively insignificant compared with that of animals. But Chironomidae[19] have been found at 49°C in the hot springs of Yellowstone Park, some Cypridae (which are small ostracod crustaceans), have been recovered at 50°C, and Rotifers at 65°C. The two most remarkable discoveries of thermophilous animals are those of the crustacean *Thermosbaena* in the hot springs of El Hamma (Gabes, Tunisia) between 44°C and 48°C and that of the Syncarid *Thermobathynella* at 55°C in a cave in the Congo. There is no doubt that such a mode of life necessitates numerous adaptive specialisations in the form of an enzyme system which has to be resistant to inactivation by heat; however, detailed researches have not been carried out on these species.

The abyssal environment

The abyssal environment is the extreme environment *par excellence* in which animals of very varied groups are found living under special conditions of darkness, temperature, and nutrition. Doubtless most of the abyssal animals were originally derived from types which evolved within the boundaries of the continental shelf, but all have been greatly modified by their new living conditions. Abyssal incongruity of form[19] is a characteristic trait of the inhabitants of this environment; for low temperatures and the absence of light profoundly affect the functioning of the glands, and this perhaps explains the monstrous forms of some of these creatures whose various organs seem to have developed in a completely anarchical fashion in relation to each other. This phenomenon is most apparent amongst the fish in which the abyssal forms appear as caricatures of those with which we are most familiar, e.g., the monsters whose enormous mouths are capable of taking in enormous prey. These creatures of the depths are also endowed with specialised senses, eyes, and luminous organs, the structure of which has been so often mentioned that no more need be said about them here.

It is strange that whilst research has continued harmoniously for several decades in the abyssal world as a whole, the fauna of the great deeps has remained relatively unknown. It is only very recently that new equipment has made it possible to dredge and drag in these depths. The recent expeditions of the Danish ship *Galathea* and of the Soviet ship *Vitiaz* are already part of history; for their records have revealed the existence of highly original zoological types, such as the mollusc *Neopilina*, which has retained the traces of primitive segmentation, and thus makes the concept of a common origin for worms and molluscs more acceptable. From the geographical point of view, perhaps the most significant result has been the realisation that the great ocean trenches are more distinct from the rest of the abyssal kingdom than was formerly thought.[20] The most common characteristics among the animals of the great trenches are lack of colouration of the body, the absence of eyes, the frequent occurrence of spines, the slight degree of calcification and the enormously elongated appendages and gigantism which affect a large number of species. Many of these characters are appreciably different from those seen in ordinary abyssal animals and indeed recall those observed among cavernicolous[21] species when the latter are compared with those on the surface of the earth. It is probable that the fauna of the ocean trenches has a very ancient origin and it seems reasonable to suppose that it became differentiated as far back as the cainozoic period perhaps 100 million years ago.

The crustacean Thermosbaena mirabilis *Monod is adapted to life in very warm water, between 42°C and 48°C.*

---

(15) Pelagic larval forms: *larval forms which live in the open sea and are free-swimming.*

(16) *Among these relics of ancient times are the Foraminifera (see note 17) from the deep inland waters, such as have been found in Algeria, Germany, Rumania, Slovakia and Turkestan. Also of interest are the small Syncarid crustaceans which differ little from their ancestors of the Carboniferous period.*

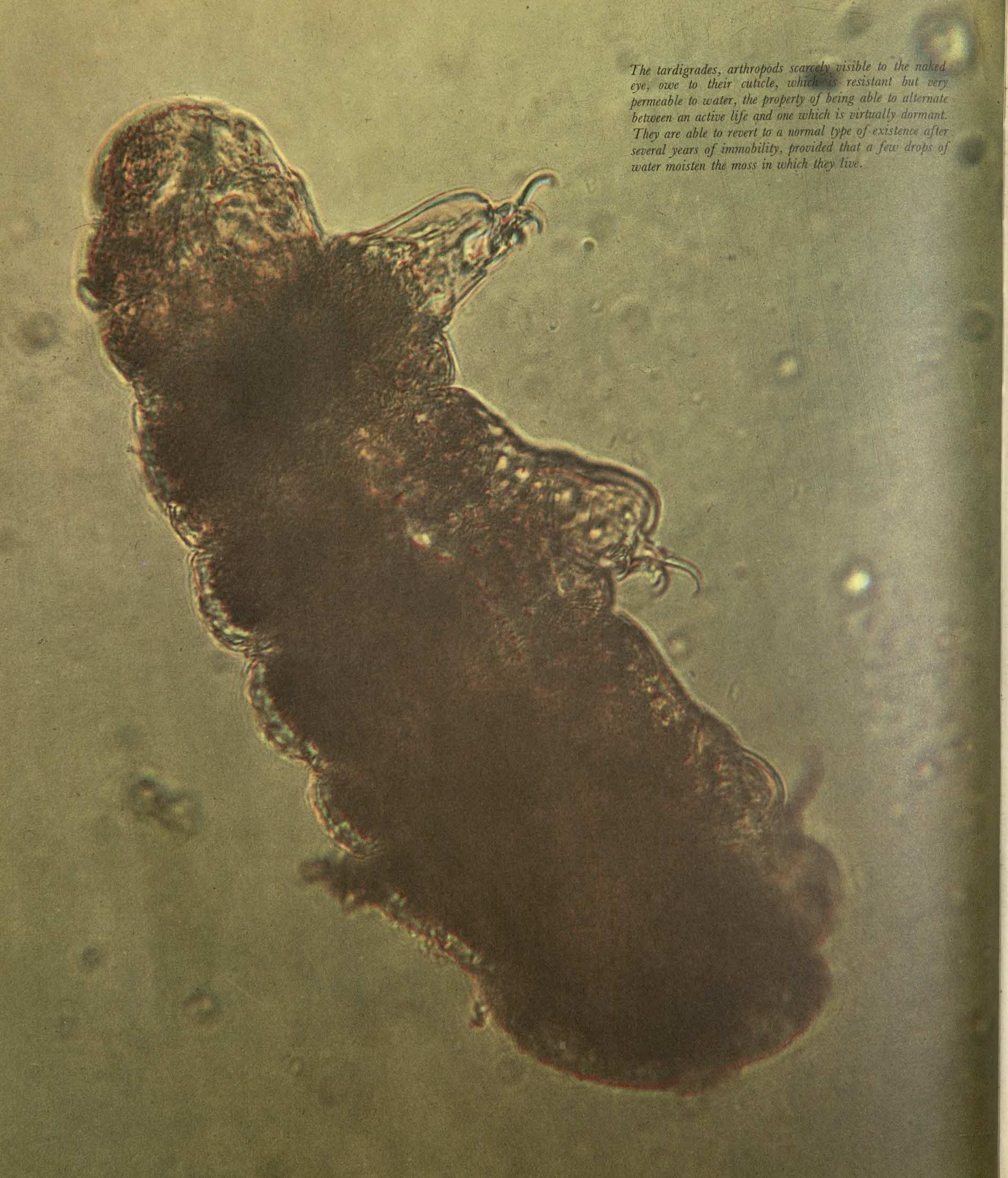
(17) Foraminifera: *small unicellular animals enclosed in a flattened shell which is often perforated with numerous holes.*

(18) Chironomids: *gnats whose larvae live in fresh water.*

(19) Abyssal incongruity of form: *unusual development due to the special conditions of life at great depths.*

(20) *Each of these ocean troughs is completely isolated from the others. Consequently, each is a kind of submarine 'island' of life cut off from its surroundings. For this reason the fauna of the troughs cannot be studied in conjunction with that of the ocean in general.*

(21) Cave-dwelling animals: *specialised forms, usually blind, which live permanently in the darkness of caves.*



The tardigrades, arthropods scarcely visible to the naked eye, owe to their cuticle, which is resistant but very permeable to water, the property of being able to alternate between an active life and one which is virtually dormant. They are able to revert to a normal type of existence after several years of immobility, provided that a few drops of water moisten the moss in which they live.

Resistance to death

Raoul M. MAY

We are accustomed to thinking that an animal has only two alternatives, life or death. However, certain disturbing facts make us wonder whether there may not be intermediate states between life and death, which are neither one nor the other. ÉMILE GUYÉNOT

We know that for twenty-seven years, between 1912 and 1939, Alexis Carrel of America, was able to keep alive by repeated subculturing[1] a line of fibroblasts[2] originally derived from the heart of a chick embryo at the seventh day of incubation.

The real significance of this experiment is that the body cells of the higher vertebrates, like those of the ciliated protozoa studied by Maupas in the last century, are potentially immortal. If protoplasm is placed in ideal conditions for the renewal of its external and internal environments, it shows no signs of ageing; for this occurs only in complete organisms which are not adjusted to their external environment. This provokes disequilibrium in their internal environment.

From this disequilibrium result, shock, injuries, or the accumulation of products of metabolism which are either toxic or merely useless waste-products which clutter up the cells. Thus the varying life-spans found in different groups of animals are related to their capacity to tolerate for longer or shorter periods these internal imbalances which lead inevitably to ageing and death.

The example of the dehydrated tardigrades

The study of resistance to death can only be pursued profitably by the observation of organisms which are successful in resisting the effects of external wear and tear and even suspending their action.

Some fairly complex animals such as rotifiers, nematode worms and tardigrades, the bear or sloth animalculae which live among mosses and lichens, are all capable of passing into a state of suspended animation when their surroundings dry up. Protected by their cuticle or skin, the internal body cells actually undergo a regressive change, and dried tardigrades are little more than small thin flakes, roughly the shape of a flattened barrel and the colour of sand. In this condition they can remain for more than six years, retaining the ability to come back to life when the absorption of water puts an end to their anhydrobiotic[3] or anabiotic[4] state. To set this process into action all that is necessary is to add a drop of water to the material to which the dried tardigrade is attached, when the body and legs swell very quickly on contact with the water. However, even when the state of desiccation has lasted only a few days, actual movement does not take place for several minutes. Nevertheless the cellular transformation[5] occurs very rapidly. In dried nematodes which have been put into water the nucleus and mitochondria[6] are already approaching the normal active state after a minute, and may be considered entirely normal after two.

The suspension of active life and cellular revival are thus accepted facts even among invertebrates which are relatively highly organised, such as the tardigrades, which possess a central nervous system and muscles. But these facts give rise to further questions: to begin with, is there an actual interruption of life followed by a genuine resurrection, or does life continue in the dried-up cells, but at a greatly slowed-up level of metabolism?

Revival or slowed-up living?

Baumann (1922) clarifies the two viewpoints as follows: according to the first, the conditions of the environment, such as the temperature or the composition of the air, have certain limits within which the normal metabolism of organisms takes place. But these limits are not the only possible ones for the

(1) Subculturing: *this consists in removing from time to time a minute portion of a tissue-culture and transplanting it into a new medium where it will continue to grow.*

(2) Fibroblasts: *connective tissue cells which have remained young and divide actively. In the embryo the mesenchyme consists mainly of fibroblasts. The differentiated connective tissue cells of adults are called fibrocytes.*

(3) Anhydrobiosis: *existence in the total absence of water.*

(4) Anabiosis: *interruption of the vital functions followed by a return to life.*

(5) Cytological transformation: *a change in the cells from a latent to an active state.*

(6) Mitochondria: *organs in the substance of the cell which are the seat of respiration and protein synthesis.*

Rotifer in its extended state. (Mag. × 800. Photo Lod).

organism regarded as a chemical system. This chemical system is thus able to pass into a stable state beyond the boundaries of life in general. When the conditions of life return to normal again, by the action of such factors as water or oxygen, this stable state again becomes labile, metabolism recommences and the organism returns to active life.

The second view holds that the essential attribute of life is metabolism. This is not only an aspect of life which can be observed, but life cannot exist in its absence; when it ceases life ceases and decay begins. According to this view, metabolism is only possible under certain environmental conditions which can be clearly specified by the scientist.

Baumann accepts this second point of view; for the fact that a certain minimum quantity of water can still be found in dried-up tardigrades shows that metabolism is still possible although in such minute creatures it may not be demonstrable. There is therefore no interruption of metabolism, no break in the continuity of life, and no such thing as latent life.

Rahm (1923–1929) also made numerous ingenious researches in this field, and his own opinion was that amongst the rotifers, nematodes and tardigrades it was not a question of mere revival following existence in an anhydrobiotic state (life in the absence of water) but true anabiosis. According to Preyer, who first used the term, this means a genuine return to life after a total cessation of the vital functions. In these instances it is assumed that metabolism stopped in the dried-up state.

Life is resistant to cold

Rahm placed dried-up animals in hermetically sealed tubes which had been filled with hydrogen, helium, or argon, but, like a Röntgen tube for producing X-rays, without oxygen. After several years the tubes were opened and the rotifers, nematodes, or tardigrades exposed to water; most of them regained their activity. In another experiment Rahm placed the same dried-up animals in liquid air at −190°C for 25 hours, in liquid hydrogen at −254°C for 26 hours, in liquid helium at −271·88°C for $7\frac{3}{4}$ hours and once at −272°C, one degree from absolute zero, for three hours. At these very low temperatures chemical reactions, and therefore metabolism, can no longer take place. Nevertheless, the rotifers, nematodes, and tardigrades when slowly warmed up and subsequently moistened were soon revived. Some of them were kept at

— 180°C for more than twenty months without harmful effects.

Again, moss which had been dried in air for more than a month was cooled to — 190°C for five hours, then heated to 151°C for a quarter of an hour and finally moistened, after which active rotifers and tardigrades emerged. These had undergone a change of temperature of 341°C, and this extreme example reveals how the tardigrades are able to survive the coldest winters and the hottest summers.

Of course, the objection can be raised against Rahm's views on the interruption of life that dried-up animals cannot live indefinitely and eventually become incapable of revival. This would not apply if life had completely ceased in the dry state, since under these conditions the time factor would be irrelevant. We know, too, that dried-up tardigrades cannot stand a temperature in excess of 100°C for long and still be revived. But to these arguments Rahm replies that the effect of these harmful factors on the dried-up animals is not on their metabolism, which no longer exists, but on its physical basis, that is, on protoplasm itself. This, which still remains in a colloidal state even when the animal is dried, would be altered in an irreversible manner by physical or chemical factors such as simple changes in temperature, or the evaporation of the minimal quantity of water which is one of its constituent elements. If this had happened, then the addition of water would no longer bring the dried protoplasm back to life.

Such considerations go beyond the deductions we can reasonably make from Rahm's experiment. But the fact remains that he succeeded in keeping his dried-up animals at temperatures so low that metabolic reactions could not possibly have continued. This is certainly an argument in favour of the old school of thought which believes in genuine revival, in a re-establishment of vital processes which had ceased in the dried-up state.

Life is resistant to the vacuum

More recently, in 1948, Paul Becquerel took up this type of experiment once more. Lichens and green algae were well dried, together with their usual fauna of rotifers, nematodes and tardigrades, and placed in glass tubes evacuated to such an extreme degree that no water vapour could remain, before the tubes were sealed. What he discovered was that these plants and animals regained activity when moistened after six years in this state, even when they had been additionally subjected to the low temperature of liquid air (— 189°C) for two weeks. Now, according to this author, under such conditions protoplasm becomes entirely solidified; it has lost any free water and gas that it may once have contained and is no longer even colloidal.

Yet, after thawing-out, the protein molecules are capable of reuniting with water and, after absorbing the necessary energy, the physico-chemical phenomena of life start all over again. Becquerel's view is that if the highest vacuum and the lowest temperatures are maintained anabiosis can continue indefinitely. Protoplasm that is solidified, dried, frozen, and kept away from radiations appears to be completely stable. It could be that under the several thousand feet which enshroud the South Pole there exist germs and frozen organisms still capable of coming to life.

Clearly these facts push back the limits of life. They can be used to support the hypothesis that specialised vegetation may exist on the planet Mars, which would explain its seasonal changes in colour. As we can see from Becquerel's experiments, neither the extreme rarefaction of the atmosphere, nor the temperatures, which vary between — 100°C and 30°C between day and night or between winter and summer, could prevent the existence of a flora of cryptogams (mosses, lichens, etc.), and a fauna of those small creatures which are able to alternate between quiescence and revival.

In 1894 Alfred Giard made a list of those organisms which can 'live' in a stage of anhydrobiosis, or latent life in a dried-up state. Besides those which we have already mentioned there are the spores of numerous cryptogams, bulbs, the sclerotia of fungi, the eggs of various crustacea which are laid in marshes that dry up rapidly, the eggs of many invertebrates with thick shells, the nymphal forms of certain insects and many terrestrial molluscs that can, by progressive dehydration, be brought to a state of anhydrobiosis which, on occasion, may last as long as seven years. Finally, among the vertebrates we have the remarkable case of the aestivation of the dipnoan fish, *Protopterus*.

What can we learn from cytology about the two theories relating to revival which have just been described: that is to say, either discontinuity or the continuity of metabolism in the dormant state? We have carried out a cytological study of the drying of the intestinal cells of the nematode worms (1942) and of the body-fluid corpuscles[7] of tardigrades (1947)

The Nematodes, or round worms, have a non-segmented body with no appendages and are covered with chitin. Certain microscopic species like this one, which has been enlarged one hundred times, possess the ability to revive after desiccation. (Photo Lod).

and in each case we found a strong basophilia,[8] associated with a disappearance of the nucleoli[9] and of the chrondriosome.[10] The alteration in the shape of the dormant cells and their intense basophilia do not help us to decide in favour of one hypothesis or the other. The fact that in certain cases the food reserves remain in the body cavities even after drying appears to favour the theory of continuance of metabolism in the dried state, since they would naturally help to keep it going.

But the considerable damage done to the nucleus and the chondriosome of the dried cells are incompatible with the thesis of the continuation of metabolism unless this has become almost independent of the elaborate structure upon which it normally depends. The disappearance of the nucleolus which melts into the rest of the chromatin,[11] the transformation of the normal chromatin structures into a solid mass, the hyalinisation[12] of the rest of the nucleus, and the total disappearance of the chondriosome combine to transform the dried-up cell in a quite fundamental way. If we believe that the cell still continues to metabolise, even at a slower rate, then we must also agree that in the normal state the usual cell structure serves only to stimulate a metabolism which can carry on with an altogether different cytological structure. The structural reversibility of the dormant cell when it is moistened suggests that in the hydrated state there develops a totally different physiological phase from that which existed previously.

It seems possible to envisage the state of anhydrobiosis or anabiosis as just one amongst the states in revivable organisms that can be exchanged for other phases of their life cycle, and it is probable that this particular state which involves profound changes in cellular structure also necessitates not merely a simple retardation of normal metabolism but its alteration or even total transformation.

Is the latent form of life possible for all organisms?

Another question comes to mind, when we reflect on these facts: how generalised is the phenomenon of latent or suspended animation? Is this a special case restricted to a certain number of organisms only, or is it possible to all protoplasm? As early as 1878 the great French physiologist Claude Bernard in his book *Lessons on the Vital Phenomena Common to Plants and Animals* had given as examples of organisms demonstrating the phenomenon of a latent form of life the seeds and yeasts in the plant kingdom and, in the animal kingdom, many infusorians, rotifers, small nematodes, and tardigrades.

The physical and chemical effects of drying

The drying of certain tissues and substances removed from higher organisms by Chevreul in 1819 has some relevance to the problem of life in a latent form. Tendons which had lost their normal properties on drying were found to have regained them on moistening. The fibrin of blood can lose 80% of its water when dried and simultaneously its colour, viscosity, and elasticity disappear. Yet when placed in contact with water it once more absorbs about the same quantity of water and its original properties return. The cornea of the eye becomes opaque when it is dried but transparent again on moistening.

Drying abolishes both the physical and chemical phenomena normal to the organism. But when moisture and heat are brought back to the dried-up organism, its tissues absorb the same amount of moisture that they had before desiccation and regain such physical and mechanical properties as resistance, elasticity, transparency, and fluidity. They soon regain their chemical properties: the dried enzymes become active again and the interrupted fermentations start up both inside and outside the organism.

In 1944, Carayon observed a curious phenomenon of partial drying in certain hemipterous insects such as bugs and plant-lice which ordinarily possess two pairs of wings and hibernate either by accident or under abnormal conditions. There was an almost complete drying-up of the abdominal organs and what remained of them formed a tiny mass flattened against the sternites[13], where it was anatomically and histologically impossible to recognise the various parts. By contrast, in the thorax the wing and leg muscles appeared perfectly normal, and when returned to laboratory temperatures the insects resumed their normal activity. So a marked drying-out of the abdominal viscera appeared quite compatible with life in these insects.

Thus, from all the researches mentioned here it would seem that a latent, dormant, anhydrobiotic, anabiotic state is one of the possible phases of living matter and protoplasm in general. It is a state during which all the physiological manifestations of life that we know today appear to cease.

(7) Body-fluid corpuscle: *a cell suspended in the liquid of the general body cavity of tardigrades, which is usually filled with food reserves.*

(8) Basophilia: *a property of protoplasm enabling it to fix certain alkaline dyes.*

(9) Nucleolus: *the granules in the nucleus of the cell.*

(10) Chondriosome: *the mitochondria as a whole.*

(11) Chromatin: *the specific basophilic substance of the cell nucleus.*

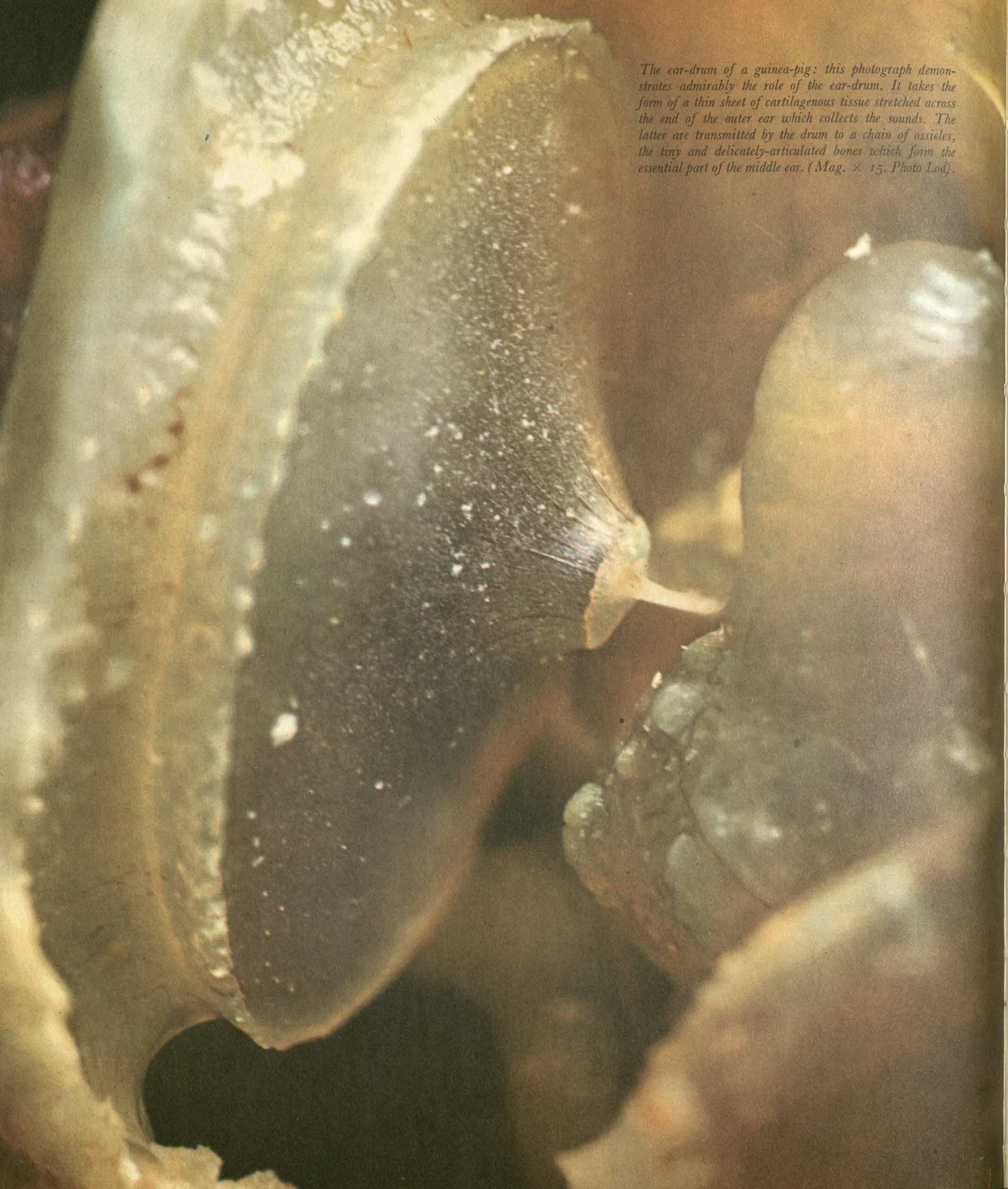
(12) Hyalinisation: *a degenerative change in the cells and other elements of the connective tissue which assume a glassy appearance.*

(13) Sternite: *the ventral plaque of the integument of an insect.*

PART TWO

The world as seen by animals

Head of a fly magnified sixty times. (Photo Lod).



The ear-drum of a guinea-pig: this photograph demonstrates admirably the role of the ear-drum. It takes the form of a thin sheet of cartilagenous tissue stretched across the end of the outer ear which collects the sounds. The latter are transmitted by the drum to a chain of ossicles, the tiny and delicately-articulated bones which form the essential part of the middle ear. (Mag. × 15. Photo Lod).

The senses of animals

C. H. FRASER ROWELL

Of all the properties of animal life, the nervous system is most clearly responsible for the fundamental differences between plants and animals. The working of the nervous system is perhaps the most challenging, and certainly the least understood, of all the fields open to the biologist who works at, or below, the level of the single individual animal. It ranges from the behaviour of the whole animal in its natural environment to the physiology of individual nerve cells. The focal point of this great array is the mode of function of the central nervous system. We know from behaviour studies the sort of things which it can, or cannot do, and we study the mechanism of the more accessible parts of the nervous system to give us insight into the properties of the components of which it is built up.

Of the component parts of the nervous system, the most easily interpreted and best defined are the sense cells. If the central nervous system be thought of as a gigantic electronic computer, and the sensory and motor nerves as conductors carrying information and power to and from it, then the sense cells are the *transducers*,[1] which translate the environment into the right sort of electrical coding to be used by the nervous system. They are at once the most essential and yet the most limited parts of the whole organisation. Without them the nervous system would clearly be useless, as it could receive no information, yet their function is completely programmed, and the behaviour of a sense cell in response to stimulation is about the most rigid form of biological response there is.

How do sense organs work? As transducers they must clearly be placed in contact with the thing they are to measure and communicate with the rest of the machinery. Thus in the animal we find the *exteroceptors*, the sense organs which relay information about the external environment, arranged on or near the outside surface of the animal. The *interoceptors*, which deal with internal conditions, are found in appropriate parts of the body, for example, the position of a limb is transmitted by one or more types of *proprioceptor*, registering tension in the muscles, flexure at a joint, stress in the skeletal elements, or displacement of sensory hairs on the surface.

Different types of animals may use predominately one of several possible alternative ways of getting the same information. The proprioceptors just mentioned, for instance, are especially characteristic of vertebrates, crustaceans and insects respectively. Similarly, there are many different ways of receiving mechanical vibrations, that is, hearing in the wide sense of the word. There are, for instance, fundamental differences between pressure receptors, such as the vertebrate ear-drum, and displacement receptors, such as the sensory hairs found on insects. One of the practical results of this is that the former animals are very good at frequency discrimination, while the displacement system permits the animal to hear a much larger range of frequencies, but to discriminate them rather poorly—it is much more sensitive to changes in amplitude ('loudness'). Even within a single animal, there are often many ways of perceiving the same stimulus. Frings and Frings recently estimated that a locust could detect noises by at least seven anatomically different methods.

Sense cells of different sorts are basically similar. All animal cells respond in a limited way to a range of environmental disturbances, such as mechanical shock, light or electrical energy, and the sense cell is merely modified to be particularly sensitive to a particular kind of excitation, and for transmitting a clear signal to the nervous system. These modifications to make the cells good transducers are usually simple and obvious, such as the incorporation of a light-sensitive pigment in a photo-receptor, or making a pressure receptor directional by stiffening it in one plane.

(1) Transducer: *an apparatus designed to receive energy from one system and transmit it (usually under a different form) to another, e.g., a microphone which converts sound waves into electrical impulses.*

One of the strange instruments of perception found amongst insects: the antennae of a moth. (Mag. × 20. Photo Lod).

But sometimes the sensitivity or discrimination achieved far exceeds either our understanding or our technical emulation. Perhaps the most striking example is the sensitivity of many male moths to specific chemical compounds produced by the female of the species. The ability of males to find virgin females from great distances has been known and used by collectors for a long time, but only very recently has Butenandt, after twenty-five years of work, isolated the first specific substance. For the silkworm moth the substance is a doubly unsaturated aliphatic alcohol of very low molecular weight, and is absolutely specific —any replacement or alteration in configuration makes it quite meaningless to the moths. Butenandt has shown that males will show a complete behavioural response to very few molecules, probably only a single one. This is a level of sensitivity of both the sense cell and the associated amplifying nervous system which is far beyond any man-made system.

The sensory organs

Especially in higher animals, sense cells are often grouped into whole organs, which permit economy and efficiency both of the nerve supply and structures such as lenses. The best examples are the well-developed eyes of creatures like cephalopods, vertebrates, or insects. Development of sense organs proceeds side by side with that of effector organs, since the one is useless without the other. Thus the most refined distance receptors are found in the more mobile animals because their environment changes faster and needs better reporting by the senses. The best mechanisms for detecting things moving at distances are to be found in animals which swim or fly, especially the latter, where fast movement in all dimensions is possible. Convergence,[3] and common physical requirements served in different ways, are characteristic of complex sense organs as well as individual sense cells. The process culminates in the eyes of cephalopods and vertebrates which superficially resemble each other, although anatomically quite different, and have been developed in different ways by animals as distantly related as it is possible to imagine.

Sensory perception is, however, by no means a function of the sense organs alone. The sensory world of an animal is as much a function of the co-ordinating activity of the central nervous system as of the sense organs themselves. All the sense cell can do is to indicate change, and rate of change, in one aspect of the environment, and the interpretation of this signal must lie elsewhere.

Take, for instance, the simple problem of locating how far away from an animal a source of stimulation happens to be—the sort of question which is of constant importance to almost all free-living animals. There are innumerable different ways of getting an answer, depending on the sense used, the kind of animal and in what sort of medium it lives, but *in virtually no case is there a sense organ which can give a direct answer.* They all demand a comparison to be made between two or more messages from the same or different sense organs.

In one or two cases these readings can be made simultaneously, as is possibly the case when two independent eyes have to be suitably adjusted in order to achieve stereoscopic vision[4] of a near object, but nearly always the information has to be compared with some obtained previously. The time interval between these readings may be short, as when an animal peers at an object, moving the head from side to side to judge the changes in parallax,[5] or when a bat echo-locates, first registering that it has made a noise, then that it has received an echo, what the interval was, and how that interval is changing with successive operations.

Equally, the interval may be very long in solving comparison with a scale of values learnt over many years. Human beings, together with other animals, can form a good estimate of near distances by appreciating the degree of accommodation needed to focus the object, even when all other clues like stereoscopic vision, parallax, learnt sizes and perspective relations, are eliminated. The importance of this last has been dramatically shown by

(2) Effector organs: *these are organs which, in contrast to the receptors, are capable of acting upon the external world (e.g., the hand).*

(3) Convergence: *in biology, convergence means a striking resemblance, even if only a superficial one, between the shape of the body as a whole, the design of various organs, or certain methods of adaptation found in species which are totally unrelated to each other (e.g., the eyes of cephalopods like the octopus and those of the vertebrates mentioned in the text, or the arrangement of the nostrils and eyes when they are placed in such a way as to remain above water whilst swimming in such widely varied creatures as the frog, the crocodile, and the hippopotamus).*

(4) *Even here it is not certain that this is a direct effect since, quite possibly, it may be an act of comparison involving memory.*

psychologists, who constructed a room in which all the normal vertical lines are tilted to a certain degree. A stranger entering such a room will himself tilt accordingly, even though several other types of sense organs, such as the labyrinth of the inner ear, are capable of providing a 'true' orientation. Similarly, he will say that any truly perpendicular object introduced into the tilted room is itself tilted. Thus we normally rely on a comparison with learnt relationships rather than make the absolute measurements of which we are capable.

Related problems are very common in animal behaviour. A deficiency in behaviour, say a failure to learn something, can conceivably be due to physiological inadequacy at one of several levels. It might be that the sense organs could not detect what was happening, or that the afferent nervous system could not transmit it effectively, which can happen if the flow of information is very rapid, or that the 'deficiency' was in the central nervous system, as in the case described above, or that it lay in the effector apparatus; the muscles and nerves in which we recognise the behavioural response. Such questions about human behaviour are of the highest importance in applied psychology, such as the study of the acquisition of skills, and are just beginning to be asked and answered. Also, and more important for our purpose, they are essential information before we can gain an impression of the 'perceptual' world' of any given animal.

Perceptual world of the animal

The perceptual world of an animal is largely determined by its sense organs, and we can get a rough picture merely by examining the quality and quantity of these concerned with different senses. However, we know how much our own perception varies among men living in different environments, or under special conditions such as the loss of one major sense. A blind man, as is well known, commonly develops his hearing and sense of touch to a much greater extent than normal people, and this alone serves to qualify the generalisation. Statements such as 'birds are predominantly visual animals', or 'small mammals rely on their sense of smell' often obscure the fact that such animals have many other ways of knowing about their environment which they can use if necessary.

The natural tendency is to compare the subjective environment of another animal with that of our own, and this allows an arbitrary classification into those animals which have roughly the same kinds of sense organs as ourselves, those which have similar sensory equipment but use them in different ways, and those which have entirely different equipment, or are sensitive to completely different kinds of environmental features. This classification is largely dependent on phylogenetic(6) relationships and similarities of structure. For example, the sensory worlds of different mammals are not basically different from our own, and many of the differences which used to be stressed are now known to be invalid or exaggerated. For long it was thought that only primates (man, apes, monkeys and lemuroids) could see colours, but there is a lot of evidence that many other groups, such as whales, rodents, and both cow and horse families have colour vision.

Clearly the relative importance of different sense systems change from class to class with the mammals. We lack the olfactory acuity of most carnivores, the all-round vision of a grazing animal, or tactile whiskers, but our eyes are comparatively good, and our own equipment is reasonably typical of mammals, enabling us to imagine their world fairly well.

On the other hand, the arthropods' structure is dominated by a hard external skeleton, through which all information from outside must pass. This has profound effects on the structure of their sense organs, and while insects have a very detailed knowledge of their environment, in many ways better than our own (for instance, they can determine planes of polarisation of light, and hear a wider range of sounds, their sense of smell is better, and their eyes, while producing less definition, see a comparable, though often different, colour spectrum and are better at distinguishing movement), they always get their information by a different method. This means that our own sensory experience can never be more than analogous to theirs, and their behaviour must perforce be judged empirically rather than introspectively.

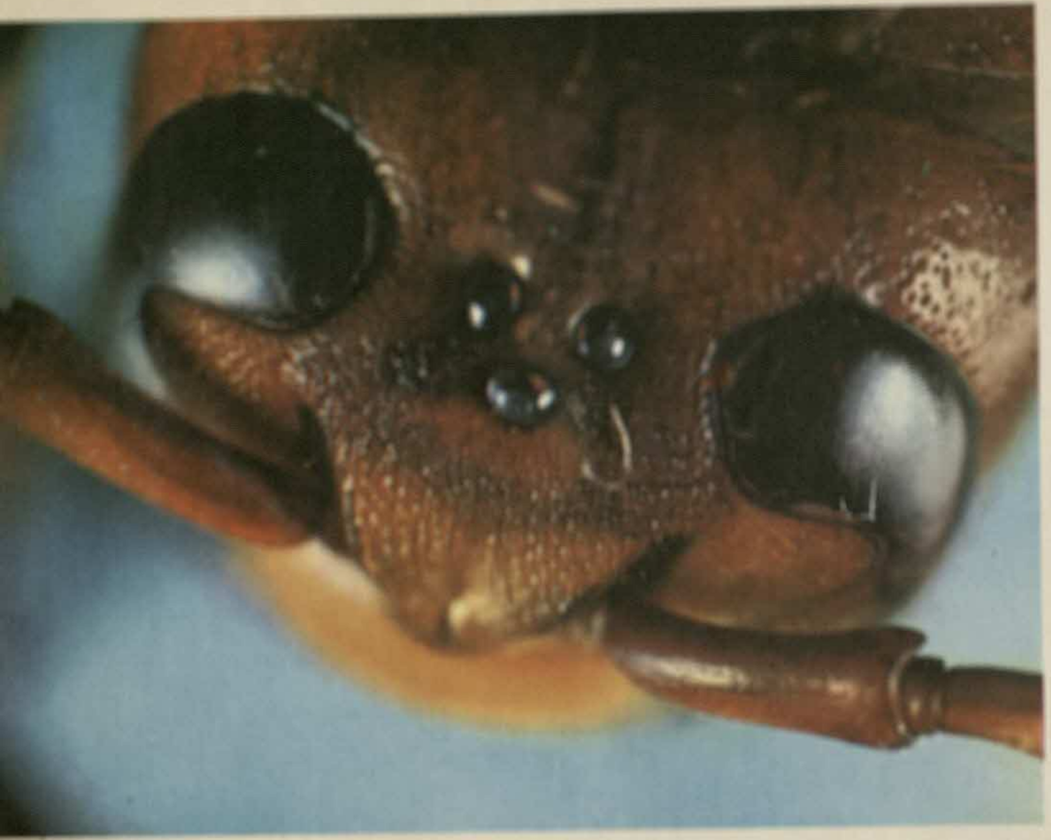
Importance of the environment

Some environments are sufficiently well defined for whole ranges of different sorts of animals living in them to show parallel sensory adaptations to a particular condition. Virtually all animals which inhabit exclusively the extreme environment of underground caves have lost or greatly reduced their eyes, and enormously developed their touch and hearing organs by comparison with close relatives living above ground. Such cave dwelling

(5) Parallax: *variations in the apparent position of an object due to a change in the position of the observer or the distance between a pair of sense organs (e.g., when one looks out of a window at a distant object with one eye closed, its apparent position in relation to the window-frame alters when looked at through the other eye. Astronomers are able to measure the distance of a star by observing its angle of parallax when the earth is at either end of its orbit (i.e., at six-monthly intervals) and, the distance between the two observation points being known, the distance of the star can readily be calculated. Animals and human beings unconsciously employ the same process by moving the head about or using each of a pair of sense organs alternately.*

(6) Phylogenetic *relationships: belonging to families related to each other from the evolutionary standpoint.*

The eye of a cephalopod (one of the most highly-developed classes of molluscs) reveals an optical mechanism capable of accommodation or focussing comparable to that of the vertebrates. (Photo Lod).



In this head of a bumble-bee we can see, between the two normal eyes composed of several thousand separate facets, three supplementary eyes which are much simpler in structure although they each possess a cornea. (Mag. × 30. Photo Lod).

adaptations are to be seen in fish, amphibia, molluscs, many insects and other arthropods, and worms.

Part of the environment of an animal is what it eats and who eats it, and the sense organs are adapted to both these factors. Predators which hunt mobile prey by sight usually have well developed stereoscopic vision, for example, praying mantises and dragon-flies, owls and hawks, cats and bush-babies. So characteristic is this that the pattern of two eyes side by side is the most important signal which releases 'mobbing' and other warning displays by small birds against predators, and it has been taken over as a protective pattern by many moths and butterflies. The sudden exposure of these 'eyespots' on the wings has been shown to deter the small birds which in their turn prey upon insects.

On the other hand, herbivorous animals subject to such predators have two widely separated eyes which give a maximum field of view all round. The retina is similarly adapted to a wide or limited area of maximum definition, or sensitivity to movement of the image. Birds, which are both preyed upon and themselves hunt moving prey, combine the all-round view with a limited area of stereoscopic vision, usually beneath the bill. The cryptic posture of bitterns, with their upward-pointing beak, also allows accurate aim if the intruder approaches within stabbing range.

Specialisation of faculties

Some animals improve their powers of discrimination in some direction until the quantitative difference from other animals becomes a qualitative one. The new function is usually concerned with spatial orientation, one of the most vital of an animal's needs. The best known of these is the echo-location system of the bat, which works on the same principle as radar, but uses pulses of high-frequency (30–100 kc/sec) sound instead of radio waves. The efficiency and accuracy of this system is partly due to the high frequencies and short intervals used, but in the most advanced forms is greatly improved by special facial structures which serve to 'beam' the sound emission, and a continuous scanning motion of the ear pinnae.

It has recently become known that similar systems are used by certain cave-dwelling birds and toothed whales (dolphins). In both these cases the frequency and rate of emission are much lower (about 7 kc/sec and 400 kc/sec), and the discrimination these animals are capable of must approach the physical limits of the systems. We can ourselves derive some information about our surroundings by listening to the echo of our speech, but this is not at all the same level as that of bats.

Another example of a special capability is the navigational system of birds. The exact mechanism of the ability of birds to return to breeding places, etc., after long migrations is still under discussion, but it is clear that the basic requirements which a bird needs are an accurate 'internal clock', and a clear view of the horizon and of moving celestial objects, sun or stars. The accuracy with which the movement of the sun has to be appreciated can be estimated theoretically, and it is very great indeed. Of all animals, only the eyes of birds are physically capable of this task.[7]

Most animals are sensitive to radiant heat, and several kinds which hunt warm-blooded prey can orientate themselves by it at close quarters, e.g., blood-sucking bugs and mosquitoes. Far excelling the performance of all other animals in this respect, however, are the crotalines or pit-vipers. These snakes have a pit on either side of the head, in front of the

(7) *See p. 109 'The Migration of Animals'.*

(8) Lateral line: *a strip of sensory organs lying along both sides of a fish which is capable both of making it aware of movement in its immediate locality and, apparently, of feeling pain when attacked.*

eyes, which is lined with sense cells unusually sensitive to this form of energy. They are good enough to be able to detect a small animal, such as a mouse, at a considerable distance (three feet) and being symmetrically arranged, can be integrated to indicate direction as well. Not only can these fantastic animals detect mammals and birds in this way, but they can also sense the presence of moist-skinned cold-blooded animals in dry air, because the evaporation taking place from the skin of an amphibian cools it appreciably below the temperature of the surroundings.

Artificial transducers

There are many kinds of perception which we lack altogether and we can only appreciate the environmental changes which they register by first interposing man-made transducers between the signal and our own sense organs. Perhaps the most spectacular example is the electric sense in some fish. Many fish can defend themselves or attack prey by using special electric organs. All muscles in the course of their contraction are associated with electric potential changes, and these electric organs are modified muscle tissue which has lost its contractile function and specialised in the production of electric potential. When the discharge of all the cells is synchronous and in series, a very large potential difference can be formed. The eel *Electrophorus*, for example, can develop some 600 volts (measured in air, less in water).

Many others, notably the tropical Mormyrids and Gymnarchids, have well-developed electric organs but do not use them this way, and it was thought that their function had been lost. Lissmann, however, has shown that these fish in fact continually emit low-voltage signals of constant amplitude and frequency (up to 1 kc/sec in some species), thus producing a standard electrical field around them. Objects other than water entering or moving within this field produce an alteration in it, which is detected by special sense cells situated in the lateral line.[8] Their sensitivity and discrimination are again very high, and the fish undoubtedly form a complete picture of their surroundings in this way. They are mainly nocturnal, inhabiting turbulent and cloudy water where eyes and normal lateral line systems would be inadequate.

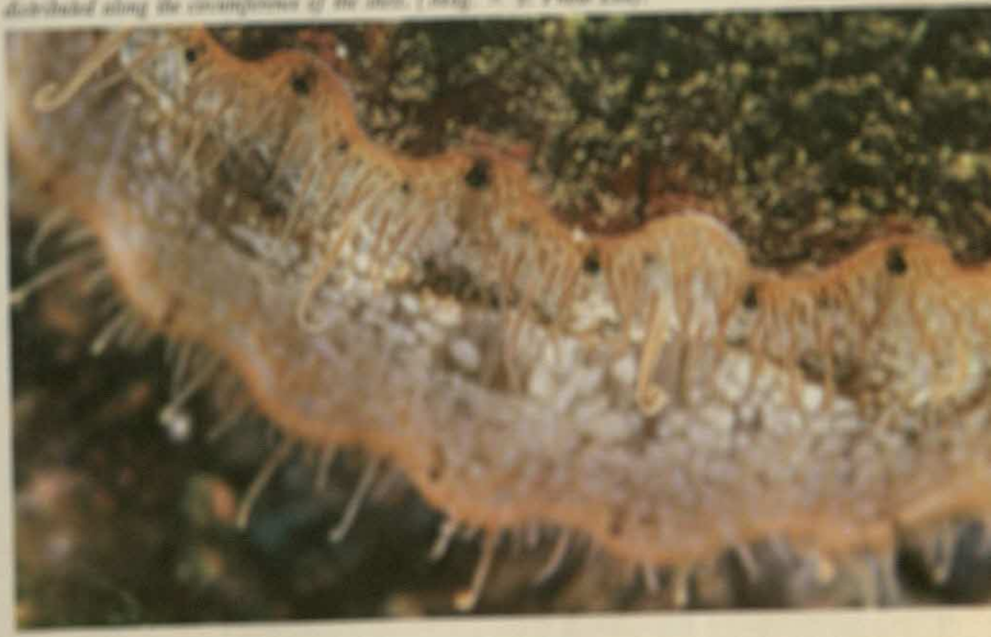
The lateral line system in other fish is very sensitive to mechanical vibrations, and enables the fish to perceive and locate accurately nearby mobile objects, or stationary objects when they themselves are moving. This alone enables them to swim and feed so successfully in total darkness, as in the great depths of the sea, or the blind cave fish mentioned earlier. It has been calculated that a mackerel can perceive a wriggling worm at about three feet.

We might also mention that many animals, such as arthropods and cephalopods, are sensitive to the plane of polarisation of light (i.e., the plane of vibration of the waves occurring perpendicular to the direction of the beam). Such animals can see a pattern of illumination in the sky or water around them, related to the sun's position, which is invisible to us. This has been shown to be important in the navigation of some terrestrial arthropods, such as bees and some isopods, but its significance in aquatic forms is still doubtful.

The senses and the social environment

So far little mention has been made of the animals' social environment. It is clear that communication between individuals must be adapted to the sensory equipment available, and the correlation between animals' social behaviour and sensory world is a vast subject which can only be touched upon here. Certain fish, for instance, fight by making rushes at the sides of an opponent. They hardly ever touch, and superficially this fighting looks 'sham' or 'ritualised' to a degree, but actually it directs shock waves at the sensitive lateral line system of the opponent which may well be quite painful.

The eyes of this bivalve shellfish belonging to the order of the Lamellibranchiata are regularly distributed along the circumference of the shell. (Mag. × 2. Photo Lod).



The eyes of the tawny owl are adapted to night-vision. (Photo Lod, from the aviary of M. Bösiger, CNRS).

The pairing behaviour of birds is dominated by the sight of the visual display of the partner and songs of complex frequency pattern, that of grasshoppers and cicadas by songs of complex amplitude pattern, and of many mammals and night-flying insects by olfactory sensation. All this fits with what has already been said about their sense organs. It is interesting to note that the auditory sensitivity of men and mice both reach peaks corresponding to the normal frequency range of their own voices. Sometimes an entirely spurious impression of intelligent insight is given by the accurate keying of an instinctive behaviour pattern to a very specialised sensory input. Some nocturnal moths react to a tone of about 70 kc/sec by immobility and falling to the ground, which serves an obvious function against predatory bats.

In conclusion it should be stressed how much there still remains to be discovered about sensory perception, from natural history to cell physiology. We have no idea how many animals get the information to behave as they do. There are, for example, the remarkable ability of the limpet to home to its original site on the inter-tidal rocks, and the sense-organs of the echinoderms such as the sea-urchins and starfish, creatures of bizarre structure and behaviour, which for the most part have yet to be discovered. Perhaps the most numerous and important predators in the sea are the cephalopods, the octopus, cuttlefish, and squids, yet the only teloreceptor known to exist in them is their excellent eyes, although they abound in depths where these must be almost useless. Do they always come to the surface light to hunt? War-time submarine detection showed that well-populated areas of the sea resound with animal noises, the function of which is almost entirely unknown, but there must be animals which use them, and possess the appropriate sensory equipment to receive them. Many fish perform regular migrations, yet we barely know the relevant geography, much less their methods of navigation. Chemo-reception in all its forms is almost a complete mystery, and we should recall that the brain itself senses some aspects of its environment directly, for there are no orthodox 'sense organs' in our body to report on body temperature or the level of carbon dioxide in the blood although we are capable of making suitable adjustments to them.

Taste and smell in animals

Lloyd M. BEIDLER

'Taste and smell are less important to man than sight and hearing which, to him, are the fundamental senses; but it would be wrong to suppose that the same is true of all animals. The senses of smell and taste share in common the fact that the substances which stimulate them and cause them to react are all of a chemical nature', said Karl von Frisch.

Animals live in a chemical world and react in one way or another to changes in the chemical environment. One-celled animals, such as protozoans, have no special receptors for this function, but react to chemicals as a consequence of the general property of irritability inherent in all living matter. Those animals that have primitive nervous systems utilise free nerve endings possessing chemical sensitivity. These nerve endings are characterised by their low order of sensitivity and the animal usually reacts to toxic material with a negative avoiding reaction. In many forms of more advanced organisation, such as insects and vertebrates, there exist specialised receptors which are highly sensitive to chemical stimulation and the behaviour elicited is more complex than that of lower forms of animals.

These chemoreceptors are usually of two types, classified according to their sensitivity and the medium in which the chemical is carried. Man possesses olfactory sense organs, which respond to low concentrations of odours in a gaseous medium, and gustatory or taste sense organs, which respond to substances in aqueous solution. The gustatory receptors monitor the food ingested and the olfactory organs monitor the air breathed. In addition, free nerve endings are also found in vertebrates in the cornea, mucous membranes, skin, etc., which usually serve a protective function. In the interior of the organism specialised chemoreceptors may be found, such as those in man which respond to the carbon dioxide content of blood and help to regulate breathing.

The olfactory and gustatory receptors usually play a dominant role in the animal's search for food. There are exceptions, however, such as birds, which rely more heavily upon vision than taste or smell. Modern man, living in a world filled with artificial foods, relies little upon his chemical receptors for control of his diet. However, when forced to live in primitive conditions, or under the stress of certain diseases which upset the normal chemical environment of the body, even man may show behaviour similar to that of lower forms of life when presented with a selection of food. The rat made deficient in vitamin B_1 is able to select food containing this needed vitamin when offered a large choice of foods. If the adrenals[1] of the rat are removed and the sodium content of the body decreased, taste sensitivity to table salt (sodium chloride) is greatly increased and the rat is able to select an increased amount of this substance for self-preservation.

Sexual and tribal odours

The role of odour in the process of reproduction is well known to everyone. The owner of a bitch on heat need not be reminded of the importance of odour in reproduction. His home is visited, from a large area of the surrounding neighbourhood, by male dogs which have perceived the scent of the bitch and are quite willing to help prevent the species from becoming extinct. The drive is quite powerful, as is shown by the fact that the male dog will try to copulate with a dummy female containing the proper sexual scent. Reactions of the male to sexual odours is not confined to higher animals. The female gypsy moth releases a sexual scent that attracts male moths from great distances. If the antennae of the male moths, which contain the appropriate chemoreceptors, are removed, the moths are unable to orient to freshly pupated females. Even sperm may be chemically attracted to eggs, although the actual substance involved is not yet known.

Odours may play a large role in the social activity of those animals that have a highly organised society. Ants have a tribal scent which makes them acceptable to one another, whereas the scent of an intruder initiates an alarm reaction. If an ant of a given social group is washed with water or smeared with the body scent of another foreign ant, it will be treated as an intruder by the ants of its own social group. Fish also may be alarmed by chemicals released from the skin of predator fish. On the other hand, odours associated with aquatic plants may be of importance in the homing reactions of fish which revisit a given geographical area each year to spawn.

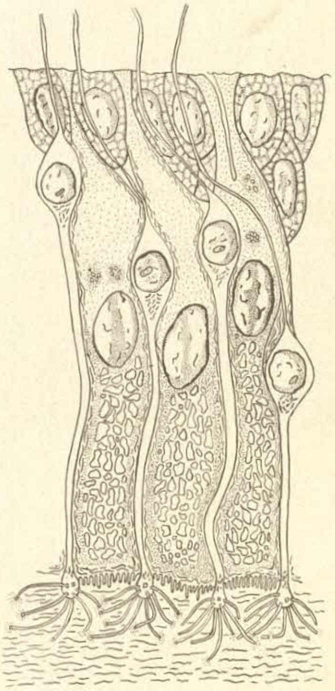


Diagram of the olfactory system in the nose of a rabbit: the long and slender olfactory cells have cilia which are spread out over the mucous lining.

Certain parasitic wasps deposit their eggs on the larvae of other insects. Some of these larvae may be buried deeply in wood so that the wasp must search the surface of the wood, using its antennae to smell the presence of the larvae. The wasp uses a needle-sharp drill to penetrate the wood directly over the larva and deposit eggs, which will then undergo parasitic growth. It is amazing to what extent insects use odours in their daily life; the sensitivity of an insect to the detailed chemical structure of a molecule is quite fantastic.

The reactions of an animal to a given odour may change with age or with previous learning. Meat is eagerly searched for by a dog only after it has had previous experience of it. Similarly, the smell of human faeces is not objectionable to children under the age of four, but is highly objectionable to a child of six or more. The association power of odours is also astounding. An adult may smell a very specific odour, such as that of freshly mown hay, and immediately recall an incident that occurred in his early childhood.

The efficient use of olfactory receptors by dogs is well known. They can trail a given individual over terrain visited by many other men and criss-crossed with previous trails of other dogs by detecting chemicals in the sweat released by a man's foot. Man also responds to these chemicals but does not utilise his olfactory sense with the efficiency shown by dogs, although the aborigenes of Australia are claimed to be quite proficient in tracking.

The senses of taste and smell often complement one another. The fine flavour of a steak is due not only to the taste-buds on the tongue but also to the odours released in the mouth during chewing, when odours enter the nasal cavity and stimulate the olfactory receptors. Most of the finer distinctions of flavour are actually based upon odour, as is self-evident when we are suffering from a cold.

Psychological and electro-physiological methods of study

How can one study the senses of taste and smell? Two approaches may be used, the choice being dependent upon the questions one wishes to answer. One may study the behavioural responses initiated when the chemoreceptors are chemically excited. Such psychological factors constitute the major portion of all studies in taste and smell, but may be quite dependent upon the physiological and psychological condition and the sensitivities of the olfactory and gustatory receptors.

Another approach concerns itself with the electrical response of the receptors or associated nerve fibres. The nerves associated with the receptors transmit information to the brain as coded messages in the form of short electrical impulses. One may 'tap in' on these nervous messages by dissecting free the sensory nerve, placing it upon two silver wires connected to an electronic amplifier and displaying the electrical nerve activity visually on the screen of an oscilloscope, when the number of electrical nerve impulses per unit time is observed to increase as the intensity of the stimulus presented to the sense organ is increased. This electro-physiological approach to the study of smell and taste results in quantitative and objective information concerning the response of the receptors that cannot be easily obtained from behavioural investigation alone.

The receptors concerned with taste and smell are usually, but not always, spatially separated in a given organism. The antennae of a butterfly respond well to odours, whereas the tarsi, or lower parts of the limbs respond to taste solutions. The nasal pits of fish, which are cavities in the head region, contain the olfactory organs, whereas the taste receptors may be spread out over much of the external surface of the body, with the highest concentration near the mouth region. In man the taste receptors are restricted to the oral cavity with the greatest concentration on the upper surface of the tongue, whereas the olfactory receptors are in the rear part of the nose. Since both receptor systems are quite distinct, let us consider them separately.

Taste

The most common structures that respond to chemical stimulation are bare nerve endings. Although these nerves are not as sensitive as chemoreceptors, they play a large role in the protective behaviour of many animals. The earthworm, for example, either retracts or curls up when it comes in contact with a noxious chemical stimulus.

In insects, however, there are specialised receptors whose endings possess great chemical sensitivity and can differentiate between various types of chemicals. For example, the receptors in the tarsi of the housefly usually consist of three cells, two of which are chemically sensitive. The receptor endings are stimulated by the chemicals that penetrate the very thin cuticle[2] that lies above the receptor endings. One of the receptor cells responds only to salts, acids and bitter substances,

(1) Adrenals or suprarenal glands: *a pair of endocrine glands situated one on top of each kidney which, amongst many other functions (e.g., the production of the hormones cortisone and adrenalin), control the sodium concentration of the body.*

(2) Cuticle: *the hard 'skin' or covering of insects, most obvious in the beetles.*

whereas the other responds to sugars. When the latter is stimulated, the mouth parts of the fly are extended to take in food. Inhibition of this extension occurs when the other receptor is stimulated by acids or salts. These two receptors, therefore, participate in a simple nervous action which allows the fly to accept or reject a chemical substance in contact with its tarsi.

Taste receptors in mammals are contained in a cluster of cells called the taste-bud, which is usually located on groups of specialised projections or papillae on the surface of the tongue. The end of the receptor nearer the surface possesses microvilli which extend into the watery film covering the tongue and thus can easily be stimulated by any substance dissolved in the saliva. The lower end of the receptor is connected to a nerve which transmits its electrical impulses to the brain. These highly sensitive cells may be damaged when subject to wide variations in temperature, mechanical pressure, and noxious chemicals. If the taste receptor or nerve is injured, the taste-bud may disappear and form again weeks later. This process in adult animals is unusual, since neither the visual nor the auditory receptors of mammals regenerate.

The four basic tastes

It is commonly believed that there are four fundamental taste qualities: salty, sour, bitter and sweet, from which all other tastes derive. Many complex tastes can be duplicated by mixing substances representative of the four taste qualities, such as sodium chloride (common salt), acetic acid (the acid in vinegar), quinine and sugar. However, there are some tastes, such as that of soap, which cannot be so duplicated. Sweet and bitter tastes are separated from the salt and sour when a leaf of an Indian plant, *Gymnema sylvestre*, is chewed for a few minutes. Sugar then tastes like sand, although the saltiness of table salt is not disturbed. Sensitivity to the four taste qualities is not uniform over the surface of the tongue. The tip of the tongue responds very well to sugars, whereas the back of the tongue responds best to bitter substances. Thus a child always licks a lollipop with the front of his tongue to obtain maximum pleasure whereas bitter medicines are swallowed quickly to decrease the duration of the bitter taste from the back of the tongue.

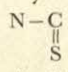
The sweet and pleasurable taste of sugars is usually, but not always, associated with nutritive material that is 'good' to eat, whereas the bitter and distasteful taste tends to be associated with toxic substances. The salt taste is important in the maintenance of the salt balance within the body under conditions of water dehydration, adrenalectomy, etc. In almost all animals a sour taste produces an avoidance reaction.

The theory of four taste qualities is only a beginning in our attempt to understand how the tongue can respond to thousands of different compounds producing different sensations. It is a useful theory, but an over-simplification of the complexities associated with taste phenomena.

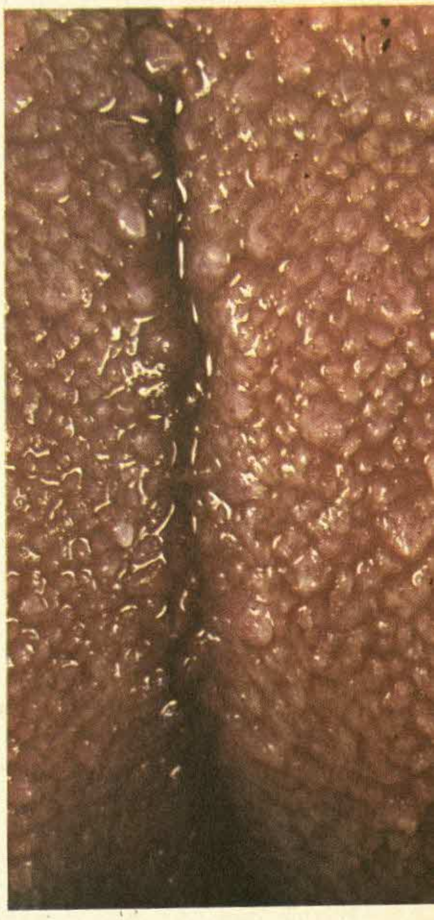
The excitation of the taste cells

How are the taste cells chemically stimulated? Most of our knowledge concerning chemical stimulation of the taste receptors has been obtained from the study of mammalian taste-buds. It is believed that the microvilli(3) of the taste cells have a surface that contains a number of areas where various types of taste molecules may be attached or bound. The receptor surface may differ slightly from cell to cell in a given species and, consequently, no two cells respond identically to a given number of taste substances. For example, some cells respond well to sugars but poorly to salts, whereas the reverse may be true with other taste cells. The binding of the taste substance to the cell is normally so weak that the taste substance can be removed by a water rinse.

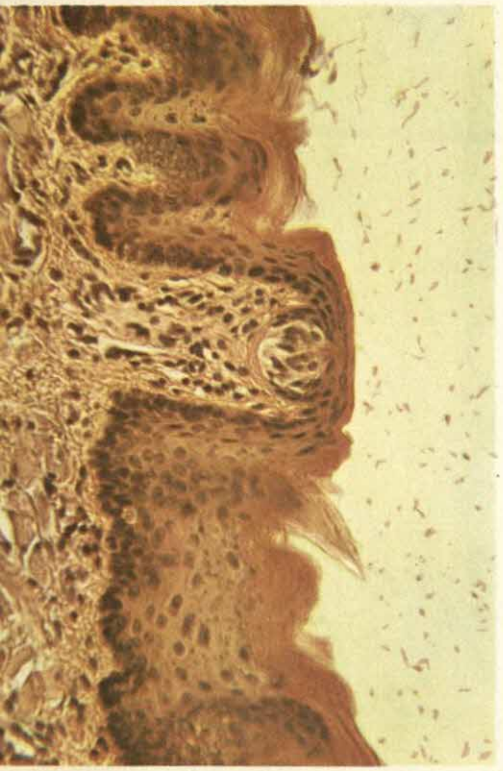
When the taste chemical comes in contact with the receptor surface of the microvilli, the taste cell, which is ordinarily electrically charged, changes its magnitude of charge and initiates electrical activity in the connecting nerve. The binding properties of the taste cell vary from one species to another; for example, the cat responds poorly to sugars whereas the hamster and guinea-pig respond very well. Rodents respond much better to sodium chloride than to potassium chloride, whereas the reverse is the case in carnivorous animals.

Since the forces that bind the taste substances to the receptor surface are very weak, any slight change in the molecular arrangement of the surface results in a difference of binding and therefore a difference in taste response. Some such differences are genetically controlled; thus it has been demonstrated that dilute solutions of phenylthiourea (PTC) taste very bitter to about 70% of Europeans, whereas the remaining 30% do not perceive the bitter taste. The differential taste sensitivity to PTC and to other closely related compounds is determined by the  $\mathrm{N{-}\underset{\underset{S}{\|}}{C}}$ arrangements of atoms in the molecules. A slight change in one

(3) Microvilli: *minute elongated projections from the surface of a cell.*



The surface of the human tongue (Mag. × 7).



Microphotograph of a section of the tongue of a rat: note in the centre of the picture a papilla with its spherical taste-bud near the surface. (Photo Beidler).

part of the structure of the stimulating molecule may change the taste completely:

p-Anisonitrile CH_3O—⬡—CN Sweet

p-Ethoxybenzonitrile C_2H_5O—⬡—CN Bitter

Smell

The olfactory receptor in vertebrates is a bipolar neuron, that is a nerve cell with different structures at its two ends. The peripheral end may contain eight or nine cilia[4] that lie in the mucous lining of the nose, whereas the central end is a nerve fibre that goes directly to the brain. In the rabbit, there are about 100 million such receptors distributed over an area of a few sq cm, in contrast to the several thousand taste receptors in the same animal.

The diameter of the olfactory nerve fibres is the smallest of any sensory fibre of the major sense organs. Because of this small size, the fibre can carry only about ten nerve impulses per second in contrast to many sensory fibres that can conduct several hundred impulses per second. This low informational capacity of a single olfactory nerve fibre may explain in part the poor discrimination of odour intensity in man and possibly other animals. On the other hand, discrimination of odour quality is very great; thousands of different odours may be distinguished from one another.

The olfactory receptors are amazingly sensitive. It has been calculated that in one sniff of certain substances there may not be enough molecules to provide one molecule per receptor. How the receptor responds to such a small number of molecules is not yet understood. The odorous molecules that are inhaled must penetrate the aqueous nasal mucosa in order to be absorbed by the olfactory cilia and the olfactory receptor then responds by increasing the number of nerve impulses per second transmitted by the olfactory nerve.

The receptors themselves do not adapt to low odour concentration although the olfactory bulb, which is the portion of the brain in which the olfactory nerves terminate, may adapt so that the intensity of smell decreases rapidly with successive inspirations. Although an animal may adapt quickly to a given odour, this does not affect its ability to respond to another odour of different quality. It is usually assumed, although not proved, that separate receptors exist for different odour qualities.

The olfactory receptors are not located in the area followed by the main air stream as it passes through the nose to the lungs. The magnitude of response of the receptors is dependent upon the flow rate of the odour over the receptor surface and is therefore also dependent upon nasal congestion and may be under control of the autonomic nerves which are under involuntary control.

No available theory of olfactory receptor stimulation is completely satisfactory. The ability to become attached to the surface of the receptor and to initiate neural activity is dependent upon the solubility of the odorous molecule in fatty substances such as olive oil, the vapour pressure, and to some extent the spatial configuration of the molecule itself. Absorption or drawing to itself of the proper molecule by the olfactory cilium is thought to lead to a disruption of the receptor cell membrane and a decrease in its permeability, which leads to a decrease in the magnitude of the electrical charge existing across the membrane. A better understanding of the mechanism of olfactory receptor stimulation must wait for additional knowledge concerning the biophysical properties of the olfactory cell. In contrast to other major sense organs, little quantitative and objective information concerning smell is now available. Electrophysiological methods have just recently been seriously used in the study of the olfactory receptor.

Two other types of nasal receptors found in many vertebrates also respond to odours. The bare nerve endings, which are distributed widely throughout the nasal cavity, respond to a large number of odours although in many cases these nerve endings are not as sensitive as the olfactory receptor. Stimulation of these nerves appears to be very important in the initiation of various reflexes that control breathing. The vomeronasal organ, an accessory olfactory organ, which is found in many vertebrates although not in man, also responds to odours. The role of this organ in animal behaviour is not known. Very few experimental studies have been performed on it and therefore its physiological properties are for the most part unknown.

In conclusion, the chemoreceptors are seen to be very important for the major functions of an animal, particularly in the lower forms where other sense organs, such as those of vision and hearing, have not yet been developed. The difficulties of stimulus control and the small diameter of the nerve fibres associated with the chemoreceptors have made the study of chemoreception very difficult. This is particularly true of the olfactory receptors in both vertebrates and invertebrates. Their high sensitivity and ability to discriminate between thousands of odorous molecules makes the study of olfaction a challenging one.

(4) Cilia: *whip-like filaments attached to certain cells or groups of cells which have a rhythmic movement that in some tissues ensures the flow of the surface mucus in the right direction and in single cells leads to movement by an action similar to that of oars.*

Releasers

Desmond MORRIS

Field naturalists have long been aware of the fact that the strange colourings, bizarre cries and weird dancing ceremonies of birds and other creatures play an important functional role in their life cycles. Without resorting to controlled experiments, these field observers automatically accepted the biological value of social animal rituals, but in previous centuries their interpretations were usually subjective and anthropomorphic. The so-called 'antics' and 'displays' were often correctly identified as specific communication systems, but the signals being transmitted were misleadingly explained in terms of human emotions.

During the early part of the present century a more objective approach emerged and in 1935 the Austrian zoologist Konrad Lorenz published his now classic work *The Companion in the Bird's World.* It was in this paper that he introduced the concept of the 'releaser' (in German, 'Auslöser').

Lorenz had made an intimate study of the behaviour of many vertebrate species and he emphasized that by comparing the behaviour of a number of closely related species it was possible to see how the various signal actions had been derived from non-signal sources. A mechanically effective action such as crouching to take off for flight, or turning to run away, might, in one species, occur in a specially exaggerated form—a ceremonial crouching, or a rhythmic ritual turning from side to side. In another related species it might have gone even further, the ceremonial crouch, for example, being now only a strange withdrawal of the neck. Lorenz pointed out that it is only by comparative studies that it is possible to trace the origins of signal actions of such a specialised type. Luckily, as different species have developed different actions as signals, it is possible to find comparatively unritualised forms of each movement if enough species are studied. These unritualised actions then give the clues to the significance of the more specialised rituals.

Any actions that were no longer concerned with mechanical problems, had lost their non-signal functions and had, in the course of evolution, become exclusive social signalling devices, which Lorenz termed *releasers.*

Releasers as social signals

In many cases the impact of these signal actions was seen to be heightened by the addition of special display structures, colours, or markings. The movement and the structure then evolved further together, producing a peak of communicatory efficiency. To use Lorenz's own words: 'Structures and instinctive actions that serve exclusively to send out key stimuli reach a high degree of specialisation, paralleling the evolution of the correlated responsive mechanisms. We have called such structures and instinctive actions, for brevity's sake, releasers.'

This concept was arrived at with the help of a great deal of practical experience gained

During certain moments of tension an animal may have a specific signal in order to communicate with its fellows and this takes the form of intention movements or releasers. This is what this bird is doing, caught by the camera during the brief moment whilst it is puffing-out its feathers. (Photo Lod).

Rosy flamingoes: the colours displayed by birds, as is shown in this chapter, play an important part in their life-cycle, especially in relation to sexual behaviour and the rearing of the young. (Photo Lod, taken in the Parc Zoologique, Clères).

from the hand-rearing of captive animals. The isolated individuals, reared in a human social environment, were repeatedly seen to perform, and also to respond to, instinctive signal actions of their own species in exactly the same way as their wild counterparts.

The idea of parent animals teaching their offspring the ways of their species began to dwindle in importance. In its place was put the Lorenzian concept of animals with a ready-made repertoire of instinctive behaviour units, both active and reactive.

Critics of the releaser concept were quick to point out that Lorenz's theorising was based primarily on observational data, rather than on carefully designed and controlled experiments. They suggested that, had his birds and fish been totally isolated from all forms of social contact, they might not then have developed the appropriate instinctive responses to the releasers of their own species. Taken to an extreme these arguments soon became highly academic. It was clear that, if the more intensive forms of isolation imposed on individual animals resulted in their failure, later in life, to respond appropriately to specific releasers, this was probably because the individuals concerned had been mentally deformed by their gross lack of experience.

The essential test is therefore one in which the animal is given as natural a development as possible, but with the complete absence of the specific releaser concerned in that particular investigation.

The experimental testing of the releaser concept was carried out in this way by a number of behaviour students, notably Niko Tinbergen and his pupils in Holland and Britain. Tinbergen developed a simple technique employing sets of dummies. Each dummy presented a different combination of releaser elements to the isolated animal and the latter's reaction was then scored quantitatively. In this way it was possible to establish not only whether the responses were inborn or learnt, but also to ascertain exactly which elements of the stimulus situation were acting as the important releasers in any given context. Many species possess several signal markings, or distinct patches of colour and it is important to establish exactly which character is operating in which context.

Tinbergen carried out experiments of this sort with a number of species of fish and birds, his most elaborate investigation being into the nature of the releasers involved in the parent-offspring food-begging relationship in the Herring Gull (*Larus argentatus*).

The case of the herring gull

He found that the young chicks of this species were stimulated to peck at a red spot on the tip of the parent's yellow bill. This pecking in turn stimulated the parent to regurgitate food for the chick. It was discovered that cardboard models of the parent's head would suffice to elicit the reaction in the chick and that if a red spot was painted onto a flat, yellow, bill-shaped piece of card, the chicks would peck at the red spot. If the spot was absent the chicks would still peck, but with a lower frequency in a given time period. It was therefore possible to design a whole series of models, each varying one small element of the stimulus situation.

Of the many tests that Tinbergen made, the following are of especial interest. Models were offered with a white head, a yellow bill and a coloured spot on the tip of the bill. The colour of the spot was different in each case. The red-spot model produced the most responses, the black-spot model was second, blue third, and white fourth. A bill without a spot was least effective. A second series was carried out in which spots were not coloured, but instead were different shades of grey, from pure black to pure white. It was found that in this case the greater the contrast between the spot (whether darker or lighter) and the bill, the greater the effectiveness of the model. This explained the success of the black-spot model in the first, coloured, series. In the next series models were offered in which there was no spot but in which the bills were of different colours. Here, the all-red bill won easily, being twice as effective as any other colour, including the natural yellow. Similar tests, but keeping both spot and bill constant, were done with different coloured heads, but here there was no difference in appeal between the different models.

It would seem from the above that the white head and the yellow bill are not particularly important in the special signal context under investigation. If the yellow of the bill is acting as a signal, it is apparently not doing so in the food-begging situation. True enough, it acts to provide contrast with the red spot, but a white bill would have done as well, or any other pale colour. The red spot on the other hand is clearly proved to be the vital releaser. It has no other conceivable function and appears to have evolved specifically in connection with the food-begging reaction.

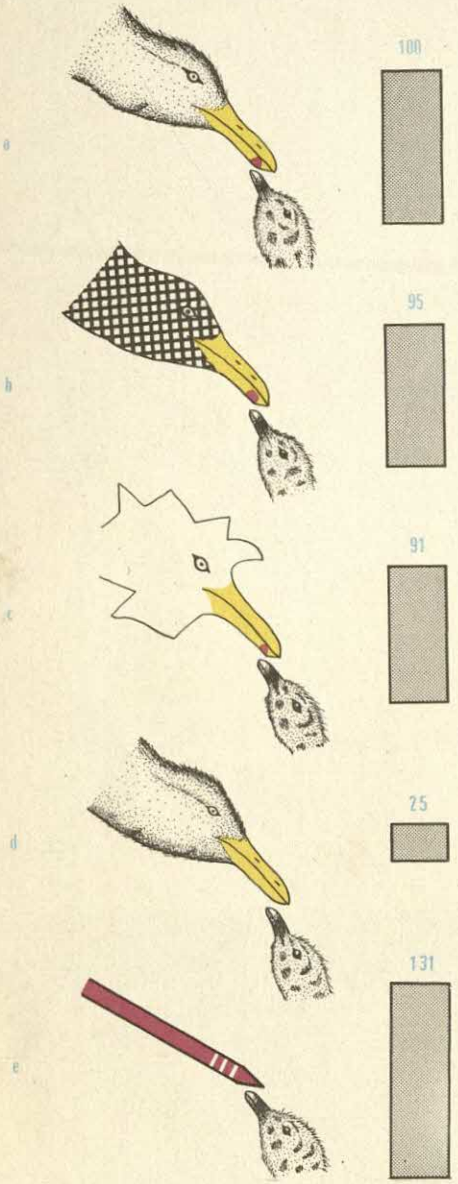
After many tests Tinbergen was able to design a super-normal model of this releaser, which consisted of three red spots on a thin wire, with no bill and no head. This was more stimulating to a chick than a real stuffed gull's head and was an excellent demonstration of the validity of Tinbergen's conclusions. Here was a case where the experimental testing, in the field, of a supposed releaser substantially verified the Lorenzian concept. Later tests by Tinbergen and his colleagues revealed that chicks hatched in incubators in complete social isolation also gave the same responses.

With a wide variety of experiments of this kind, the nature of social releasers has gradually become clearer. We now know that animals reacting to a releaser usually ignore all other aspects of the situation. In the above case for example, the head and bill were irrelevant to the begging response. In other well-known cases a similar situation has been demonstrated. David Lack found that the English robin (*Erithacus rubecula*) would attack a bunch of red breast feathers, if the latter were stuck to a wire and placed in its territory. A complete stuffed robin, but with the red breast patch painted over with brown ink was, however, completely ignored by the territory owner. In other words, in an aggressive situation, the red breast patch was the vital releaser in this species and the rest of the bird virtually did not exist. This does not mean, however, that this bird is insensitive to the detailed appearance of members of its own species. On the contrary; for the robin, like many birds, must be able to recognise minute details, in order to be able to distinguish its mate from other individuals.

A similar situation exists in the case of the three-spined stickleback (*Gasterosteus aculeatus*). Here too, there is a red patch of colour that spells aggression. Model tests made by Tinbergen showed that this situation, like the herring gull case, could be analysed quantitatively by presenting set after set of simple wax models to male sticklebacks on their territories in the spring. Once again it was possible to study the way in which only a few vital characters were operating as aggression signals.

Similar tests were also carried out with budgerigars (*Melopsittacus undulatus*), lizards of

The swelling of the turkey's wattles is an obvious example of a releaser.



Experiments on the herring gull. (a) The young bird pecks (a hundred times) at a simple model of the normal head of the adult bird. The colour (b) and the shape (c) of the head have only a very slight effect upon its behaviour. On the other hand, the red spot on the tip of the bill is important; when it is missing (d) only twenty-five pecks are registered. A small red rod with white bands, in this case a pencil (e), is even more effective than the model of the normal adult head, rating no less than 131 pecks.

various species, Cichlid fish, butterflies, and various other groups of animals. The results were basically always the same, and it emerged that releasers could be characterised in the following way:

(1) They are *conspicuous.* Any signal must be well displayed and must not be confused with anything else in the environment. Hence the 'unlikeliness' of many of the releasers and the fact that we often refer to the signalling ceremonies or structures as weird or bizarre. They *have* to be strange and eye-catching (or ear-catching or nose-catching in the case of songs or scents) if they are to operate efficiently. Just as many markings, colours and postures have been evolved in a way that makes their owner merge inconspicuously into his environment, so releasers must do the exact opposite. This is dangerous, of course, as it reveals the displaying animal to its enemies as well as to the other member or members of its own species. This problem is solved in many cases with the employment of 'transformation displays'. These are displays in which, by a process of puffing up, erecting, or spreading out, the vital releaser signals can be put on show suddenly and briefly at the vital moment. The inflation of wattles, the spread of pheasants' tails, the erection of the feathers of many birds and the erection of the hair of many mammals are good examples of this technique.

(2) Releasers are usually *simple.* There is obviously a limit to the extent to which completely inborn reactions can be, so to speak, built-in to the nervous system. The releaser is seldom complex and is usually, as already described, a simple patch, or a repetitive movement of the body. The social reactions to more complex situations are typically those that have been learnt by the individuals during their lifetime. Notable exceptions are such cases as the peacock's tail. Reaction to this appears to be of the normal, inborn, releaser type, and yet the details of the tail markings are incredibly complex. This exception has not, at the present time, been explained.

(3) Releasers are *specific.* Each species has its own secret code of signals, and tests with closely related species indicate that there is often a great deal of releaser divergence in otherwise rather similar species. Tropical finches, for example, are known in literally hundreds of forms and they are all distinct species, but if they were robbed of their bright releaser markings and their display dances and calls, it would be practically impossible to distinguish them one from another.

(4) Releasers are *inborn.* Recent experimentation has shown more and more clearly that Lorenz was correct in his original assertion that releaser actions and the responses to them do not require any special learning process during the individual's lifetime. Only very drastic distortion of the early lives of individual animals can interfere with these inborn responses.

(5) Releasers arise in the course of evolution *from tension responses* of one sort or another. It is in moments of tension that animals have something important to communicate and it is the basic responses to tension that are therefore available as bricks out of which the releasers can be built. When an animal is in a tense state of conflict there are a number of characteristic responses it makes, such as intention movements, ambivalent movements, displacement activities, or autonomic shock reactions. It is these responses that have usually been ritualised in the course of evolution into the releaser ceremonies we see today.

Intention movements and displacement activities

Intention movements of starting to jump away, turn aside, or take off, have often become ritualised as crouching, stretching, swinging, turning, or wing-spreading releasers. In their new signal roles it is often difficult to tell that they were once simple intention movements of the kind a boxer or an athlete makes when he is about to start a vigorous movement. Ambivalent movements are similar to intention movements, except that they involve a rhythmic moving back and forth. These signals are most important as the basis of a great deal of so-called animal dancing.

It is also noticed that during moments of tension there are a number of apparently irrelevant actions taking place and these, the displacement activities, have also been modified for signal functions in many species. Many birds, for example, fiddle with nest material during tense social moments. This displacement nest-building has, in certain species, evolved into a special straw-carrying ceremony that has now become a significant releaser ritual during pairing and courtship.

The plumage of birds, which we often admire for its rich or bizarre qualities, in fact plays a fundamental role in behaviour and adaptations to their environment. It is at one time a signal, at another camouflage.

Autonomic changes in the respiratory, alimentary, circulatory and thermo-regulatory systems also occur at moments of tension and these have been ritualised in a number of ways. Respiratory changes have led, through a long process, to the complex vocalisations we know today. These probably started out as simple gasps and hisses of the kind that can still be heard in the case of many reptiles. But these simple noises have become specialised as auditory releasers in many groups of vertebrates. Alimentary changes such as sudden urination or defaecation have led to the use of urine and faeces as olfactory releasers, notably amongst mammals such as the carnivores, but also in many other groups. Circulatory changes have led to social signals based on flushing of bare skin patches, or sudden pallor. Thermoregulatory changes have led to the already mentioned feather and hair erection displays. These have been used extensively by many species and one only has to think of the tremendous variety of crests, plumes and manes that exists among birds and mammals to realise how important the ritual specialisations of simple overall feather or hair erection have been. The ritualisation of thermo-regulatory sweating in mammals has also played a basic role in the evolution of olfactory scent releasers.

In addition to the specialisation of these various movements and postures, there have been added in many cases the extra signal attraction of bright colours or markings. Although experimental work is progressing at an increasing rate, there are thousands of examples that have, as yet, not been studied in even the simplest way. Every patch of colour, every ritual, is available for objective analysis in the manner described here and, although the releaser concept is now irrefutably established both observationally and experimentally, it is to be hoped that in the years to come a wider and wider range of data will become available from an increasing number of animal species.

Social hierarchies

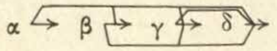
Martin W. SCHEIN

If several cows, strangers to each other, are placed together in an enclosure, the probability is very high that there will be a great deal of scuffling, pushing and fighting among them. Soon, however, perhaps in a few hours, the fighting and excitement will no longer be evident and the cows will appear as peaceful and quiet as usual.[1] *The fighting accompanied the act of establishing a social hierarchy, while the quietness afterwards reflects the effect of an hierarchy after it is established.*

The hierarchy governs physical interactions between each pair of animals in a group, and although it is responsible for intense fighting at first, it actually tends to minimize disturbances and excitement afterwards by reducing fighting and friction. Once established, it permits the animals to unite into an orderly cohesive group rather than a collection of individuals acting independently.

The order of dominance

The simplest form of social hierarchy is called a *straight-line dominance order*. In this arrangement, one individual, the *alpha* animal, dominates all the others in the group. The alpha animal avoids none of the others in any situation, such as during feeding or mating, since there are none that can beat it in a fight. The next individual, the *beta* animal, similarly dominates all individuals in the group except the alpha animal. The *gamma* animal dominates all except the alpha and beta animals, and so forth down the line to the last animal, the *omega* individual. The omega animal wins no fights and therefore submits to or avoids all the others.[3] Thus a straight-line dominance order is represented graphically as:



or more simply as: $\alpha \rightarrow \beta \rightarrow \gamma \rightarrow \delta \rightarrow \omega$

where the arrow points from dominant to submissive animals.

The most common deviation from a straight-line dominance order is called a *triangle*. It occurs principally in groups of many individuals rather than among small groups. As an example, a triangle occurs when alpha dominates beta, who dominates gamma, who in turn dominates alpha. The triangle may occur anywhere along the dominance order, and need not necessarily involve adjacent individuals.

Thus:

$$\begin{tikzcd}
 & & \gamma \arrow[dr] & & \\
\alpha \arrow[r] & \beta \arrow[ur] & & \delta \arrow[ll] \arrow[r] & \omega
\end{tikzcd}$$

and:

$$\begin{tikzcd}
 & \beta \arrow[r] & \gamma \arrow[dr] & & \\
\alpha \arrow[ur] & & & \delta \arrow[lll] \arrow[r] & \omega
\end{tikzcd}$$

are triangles. Actually, triangles occur so commonly that the term *dominance order* rather than 'straight-line dominance order' is more frequently used by biologists.

Another variation from the simple dominance order has been described among pigeons. Subordinate pigeons frequently tend to peck back when attacked, and not uncommonly win over the dominants, especially if the fight occurs in or near the subordinate's roosting area. Dominance in this situation simply means the percentage of peck encounters won: if pigeon A out-pecks pigeon B in more than 50% of their encounters, then A dominates B. This phenomenon is termed *peck dominance*, in

(1) *Much of the credit for the early work in social hierarchies goes to a Norwegian, Thorleif Schjelderup-Ebbe, who in 1922 described dominance orders in domestic fowl. In the United States Allee and his students in the 1930's and 1940's greatly expanded our range of understanding of the principles of social dominance among a variety of species. The list of species which exhibit a straight-line dominance order or a simple variant is extensive and ever-increasing, and includes many mammals, birds, reptiles, fish and even crustaceans. As a representative sample of the species investigated we may mention primates, cattle, carnivores, rodents, canaries, chickens, tortoises, sunfish, and crustaceans. From such studies of individual species, behavioural scientists have been able to ascertain phylogenetic trends and general principles underlying the mechanics of social hierarchies.*

(2) Phylogenetic: *pertaining to the evolution or ancestral history of a group of animals.*

contrast to the 'peck right' in chickens wherein the subordinate invariably avoids or submits to the dominant.[4]

Identification and concurrence

The phenomenon of social hierarchies depends to a large extent upon the ability of a group member to distinguish between other individuals in the group. Such an ability has not been clearly demonstrated among the lower forms. In the social insects, such as bees and ants, each colony member can distinguish between members of its own colony and the other colonies, and perhaps between members of its caste and other castes within the colony. However, an ant or a bee does not seem to be able to distinguish between other ants or bees of its caste, and so a clear-cut dominance order among individuals is usually impossible. However, a social dominance hierarchy has been described among the several females of an Italian wasp during the winter. In this instance, the dominance relationship establishes an order for the division of labour and thus proves of direct benefit to the survival of the colony.

Memory plays an important role in contributing to the stability of a dominance order, especially in large groups where individuals are not in constant daily contact with each other. Chickens and rats, when separated from well-established hierarchial groups, will regard their former group-mates as strangers if the separation lasts as little as six weeks. Cows, on the other hand, can remember their positions in the social hierarchy after a 6–9 month separation. By the same token, it has been shown that alterations in the appearance of a chicken, especially in the head and neck region, render it unrecognisable to its flock-mates and it is attacked as a stranger.

It is possible that the relative benefit derived from the alpha position also contributes to the stability of a dominance order. In dairy cattle the alpha cow enjoys no special benefits from her position: food is usually abundant and everyday needs are provided for. Therefore, relative rank positions of cows in a herd change little during their lifetime: they are dominated by the older, more senior members of the herd, and in turn dominate the younger or junior members. As the oldest cow dies or is removed, the next oldest member of the herd automatically moves up to alpha position.

However, when competition for the essentials of life is keen, the alpha animal derives special privileges from its position, the most and best foods, free access to water, first and perhaps only choice of females,[5] and so forth. Such a situation causes a relatively unstable rank-order, since the persistant attempts by lower-order animals to secure a share of the limited resources available leads to continual clashes. Thus, the alpha position among a group of wild rats goes only to the strongest and most vigorous individual. There is a continual turnover as young individuals reach the peak strength and agility of maturity and usurp the dominant position over their elders, who are then relegated to a position far down the rank order scale.

Determination of the hierarchy

Many factors are involved in determining the rank position of an individual. Several of the more important ones are listed below, although usually the outcome of a specific fight (and therefore frequently the rank position itself) depends upon a complex of factors operating together.

1. *Seniority.* In the more stable rank-orders where competition for the necessities of life is not intense, seniority plays a major role. The senior animal has gained dominance over its juniors when it was quite active and vigorous, and thereafter junior members do not challenge it, despite the fact that the senior may have since become weakened by age and no longer able to withstand serious challenge.

2. *Strength.* Usually, strength depends upon the weight and physiological state of the animal. A healthy individual has a better chance of winning a fight than does a sick animal. In some of the lower vertebrates, such as fishes, turtles and lizards, the heavier or larger individual will usually win. However, among the birds and mammals, weight *per se* plays a minor role in the determination of successful encounters.

3. *Experience.* Individuals who have gained a certain amount of skill and agility from previous fights are more likely to win against their less-experienced brethren. Also, those with the recent experience of repeated wins are strongly favoured over those with a history of repeated losses.

'Experience' is not solely limited to an animal's history of successful or unsuccessful encounters, but may involve a variety of environmental influences during a specific social situation. For example, peck orders among chickens were changed by the use of

For the zoologist studying animal hierarchies, the poultry-yard is an ideal object of study: the establishment of an order of dominance appears as a confused scene, the significance of which is only apparent to the experienced observer. (Photo Lod).

(3) *A common system of presenting rank order data is to tabulate the number of times an animal dominates or submits to others during encounters. Domination or submission need not necessarily include actual physical contact, so long as the result of the encounter is clear. A typical form for such a tabulation is shown on p. 85. In a straight-line dominance order, the animals can be listed so that all the fights are accounted for on one side of the diagonal.*

(4) *Other terms synonymous with dominance order are often used in conjunction with certain species. For example 'peck order' is used with reference to chickens and birds, and not infrequently to describe dominance orders among mammals and fish; 'barge order' and 'hook order' have both been used with reference to dominance among cattle.* Peck right *is that type of dominance relationship where the dominant animal rarely, if ever, is pecked back by a subordinate individual; thus, all the pecking encounters and attacks are unidirectional in the dominance order.*

It is explained in these pages how relationships of dominance arise in groups of animals. The hierarchies found among domestic animals are not fundamentally different from those which can be observed in creatures as far removed from each other as cows and caimans. (Photo Lod).

electric shocks to the alpha bird during pairing contests. Furthermore, it has been determined that variations in early social experiences at young ages have a profound effect upon subsequent social behaviour of adults.

4. *Sex.* Males usually dominate females. In fact, often in a mixed bisexual group, two rank orders will be established: one for males, the other for females. Yet, at the same time the lowest ranking male is still dominant over all the females. This relationship does not necessarily hold for juveniles, where the sexes may be intermixed in the rank order.

5. *Defence of young.* A female will often fight fiercely to protect her young and frequently will drive off the alpha animal, whether male or female.

6. *Breeding.* Certain varieties, strains, or breeds of a species characteristically win fights over other varieties and breeds, so that all members of certain varieties are dominant over all members of another. For example, in a pen containing both black and bronze turkeys, all the blacks may be higher in the dominance order than any of the bronzes. Similarly, strains of mice have been inbred to produce particularly fierce and aggressive animals, which invariably dominate other strains of mice.

7. *Pair associations.* It often happens that two individuals are closely associated within a group. In these instances, the rank position of the pair is determined by the position of the higher of the two. For example, a juvenile howler monkey living in close association with the mother automatically assumes the mother's rank position. Similarly, the female consort of the dominant male howler monkey assumes a dominant rank in the group no matter what her former rank had been.

8. *Hormones.* The relationship between hormones and social hierarchies is not absolutely clear. It is generally agreed that injections of adrenal, thyroid, pituitary and ovarian hormones do not *directly* affect aggressiveness of animals. However, injections of androgen[6] often result in increased pugnacity and aggressiveness and a rise in social rank in fish, turtles, chickens and ring doves. The change is especially pronounced when androgens are administered to castrated or juvenile males.

On the other hand, recent data seem to indicate that the role of androgens in dominance orders of domestic fowl may not be as important as was previously considered. Occasional males still have bits of testicular tissue remaining after an incomplete castration, and that the tissue is producing androgens is evidenced by some development of the male secondary sexual characters. However, the presence or absence of gonadal tissue seems to have little effect on the social dominance status of the birds. Again, complete castration of green sunfish did not alter their levels of aggressive behaviour.

9. *Territory.* An animal's home is his castle, and he fights best in familiar surroundings. Actually, it is difficult to separate the concept of 'territory' from the phenomenon of dominance orders. In the simplest sense, a territory is that physical area from which an animal excludes all others of its species except certain selected individuals. Thus, a male robin permits only his mate to reside in his territory, while a male fur seal defends his area against any male intruders but permits any number of females to join (but not to leave) his harem. The male Cichlid fish allows only a gravid female to enter his territory, and even she is driven away after her eggs are deposited in the nest he has built. Territorial defence is not confined only to males: female mammals viciously defend their young in the nest against conspecific and interspecific[7] intruders. Sometimes an entire group participates in territorial defence: howler monkeys live in bands of four to forty individuals arranged in a rigid hierarchical system, each band operating as a unit in defending its territory from neighbouring bands.

Inside territorial boundaries, residents reign supreme, no matter what the relative rank order positions are on neutral ground. Thus, the gamma or delta pigeon will often successfully defend its roosting area from intrusion by the alpha individual. The fighting success of a male Cichlid fish is inversely related to his distance from the centre of his territory, so that two fish at the borders of their adjoining territories are about evenly matched.

Different orders of dominance

Let us now examine the complex interaction of these factors by attempting to predict what may happen when two animals, A and B, of the same species, meet for the first time. If A happens to be of a variety that normally dominates B, then the outcome is clearly predetermined. If, however, they are of the same variety, then one must examine their histories in order to predict the outcome of the contest. If they are of unequal sizes or if one happens to be in a poor physiological state, then again the outcome is predetermined.

A parrot prevents a rival from entering his territory, represented here by a can of seeds. (Photo Lod).

---

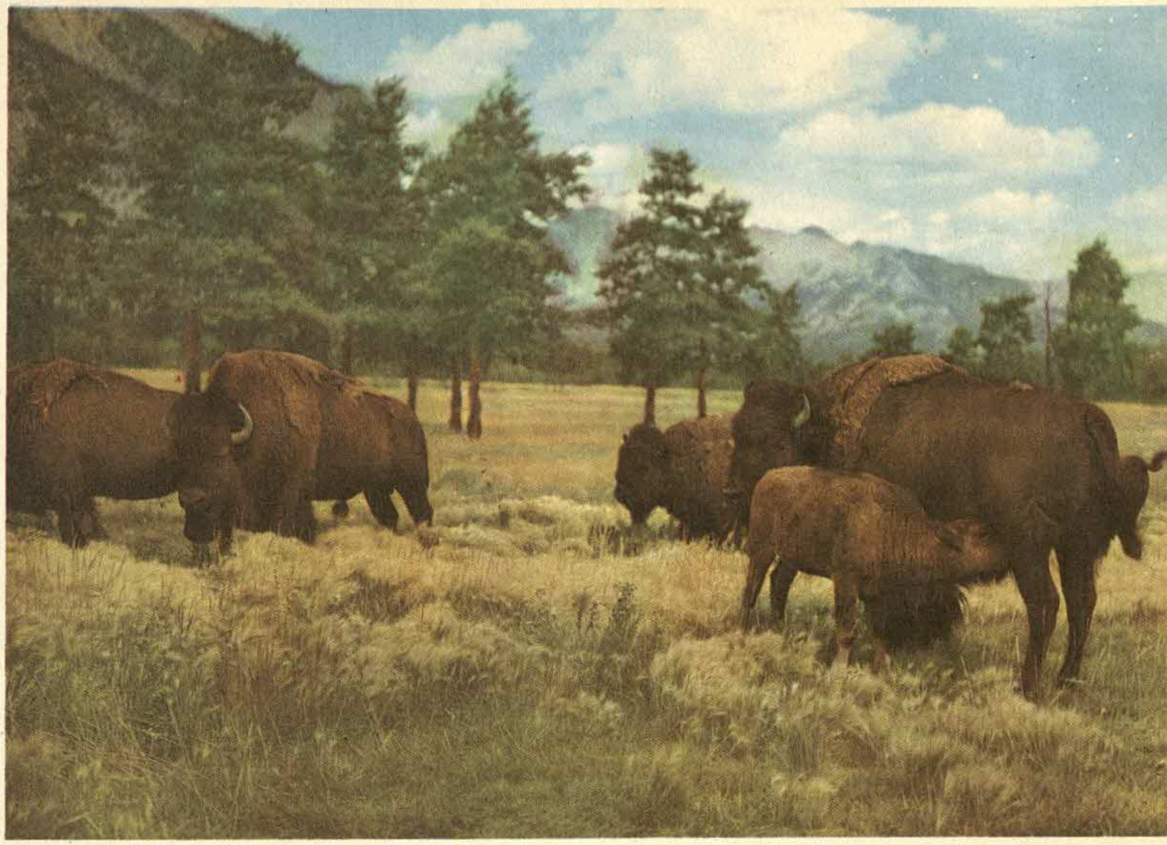
(5) *Among domestic fowl, the alpha male does most of the mating with the females. Even if he is temporarily sexually inactive, he interferes with or tries to prevent matings by subordinate males.*

(6) Androgens: - *substances which have masculinising effects on animals. Although many androgen and androgen-derivatives are known, the most familiar is testosterone, produced by the testis. It functions primarily in the induction and maintenance of male secondary sexual characters.*

(7) Conspecific: *members of the same species.* Interspecific: *between species; in this sense, members of other species, especially predators.*

(8) Intention movements: *movements which signal the onset of a behaviour sequence or activity; the sequence is not necessarily carried to completion. For example, the lowering of the dominant cow's head is one of the component movements preparatory to attack. If the other cow does not immediately submit, then the head will be lowered still more and a chain of movements, constituting 'attack' will follow.*

(9) Sibling: *one of two or more offspring from the same parents.*



Amongst all the higher animals living in groups like this herd of bison, we can observe at any one time a rigid hierarchy showing itself in specific forms of behaviour determined by such factors as age, strength, experience, or sex. (Photo Holmes-Lebel).

If it happens that A has just won a series of fights with others, while B has a history of losing fights, then A will probably dominate B. If both have a history of submitting, i.e., consistently losing fights, they will probably avoid each other, and in fact may both turn and flee in opposite directions. The first to recover from its flight will win, since it will then reverse its direction and chase the other. On the other hand, if both have a history of winning fights, then there will certainly be a fight between them and a prediction of the outcome will depend upon other factors. If one happens to be in familiar surroundings, then the outcome of the fight will be prejudiced in its favour. Even in a neutral fighting area, if one happens to be among members of its own circle, then it will probably win against an introduced stranger.

If one has been subjected to a series of fights which it won, but suffered many wounds or was otherwise exhausted, then it will often lose to an otherwise low-ranking individual. Thus it happens often that the alpha animal beats the beta individual in a severe fight, but the fight leaves it exhausted and vulnerable to the delta animal which thereby defeats it. This complex of factors commonly causes triangles in the dominance order.

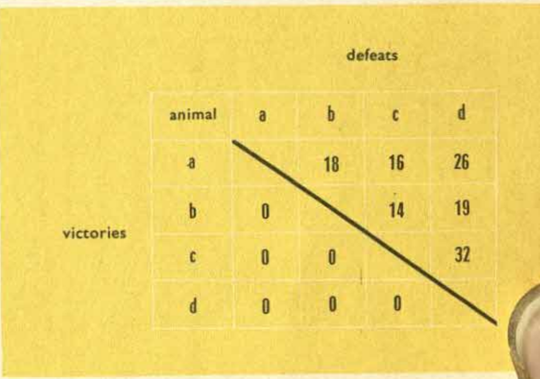
Frequently, the alpha male is continually challenged by subordinate individuals. The ensuing fight may be so severe as to exhaust both participants, who are then attacked by others in the group and one or both are displaced to the omega position. If the dominance order is characteristically unstable, as in rats, mice and turkeys, any temporary weakness or illness of the alpha male will automatically mean relegation to the omega position.

Hierarchies favour the survival of the species

Contests between individuals may be outright severe fights, brutal and relentless to the death as between game-cocks, or may be merely symbolic and involve no direct physical contact as the howling of howler monkeys or the drumming of sage grouse. Between the two extremes are many variations: the biting and tail-slapping of fishes, the barging and pushing of cattle, the clawing and wrestling of turkeys, the bobbing and squawking of herring gulls. Usually, however, these do not result in the death or severe debilitation of the loser, since it submits before that point is reached. Once the relationship between two animals is clearly established, subsequent interactions between them may be relegated to the symbolism of simple threats or intention movements: the dominant cow need only lower her head slightly and the subordinate will move away.

Minimising physical damage has of course great adaptive value to the species. Lower order animals have poorer chances of survival and reproduction, which in itself is of eventual benefit to the species. However, if some accident or chance occurrence removes the dominant animals, the highest ranking survivors are still available to perpetuate the species. The situation is quite different in fighting cocks, where selection pressure is for fights to the death, losers are completely eliminated from the species, and so such fighting behaviour is termed non-adaptive.

Concomitant with symbolised intention movement are characteristic postures, both of dominant and submissive animals. Dominant male black bucks stride in a typical manner with the head held up and ears flattened back. The characteristic postures of domestic fowl upon winning or losing fights have been recently described. One may determine the



		defeats			
	animal	a	b	c	d
victories	a		18	16	26
	b	0		14	19
	c	0	0		32
	d	0	0	0	

Position of an animal in order of dominance showing the distribution of its defeats and victories in relation to the total number of encounters. In the case of a straight-line dominance order, the figures representing the encounters are all situated on the same side of the diagonal.

relationship between a pair of animals simply by noting their postures when they are near each other, despite the fact that no fight occurs. A subordinate mouse, upon being approached by a dominant, rears up on its hind legs, raises one foreleg and closes its eyes while withdrawing the head. Usually a submissive posture will inhibit or minimize attacks by dominants. Dominant postures tend to elicit submissive responses (if not outright avoidance), or on occasion, attacks by challengers.

Despite the viciousness and brutality inherent in the establishment of dominance orders, social hierarchies contribute markedly to the survival of the species by actually reducing the amount of friction and fighting within a species. Once the hierarchy is established, and this happens quickly after the formation of a group, each animal knows and accepts its place; fighting and friction are thereafter reduced to a minimum. In a stable situation, such as in dairy cattle, actual severe fights are rare and occur only when strange individuals are introduced to the group. Otherwise, the herd lives fairly peacefully and interactions between individuals are reduced to simple threats or intention movements.[8] Flocks of chickens with well-integrated social hierarchies live relatively peacefully and produce more eggs than flocks continually disturbed by upheavals in their social caste system.

Human hierarchies

The foregoing discussion has carefully excluded any reference to man, and for good reason. Very few scientific studies of social hierarchies, dominance or territories in man have been carried out, although much can be implied by extrapolation from lower forms. It would not be at all surprising to learn that dominance orders and territorialism with perhaps a cultural overlay are common phenomena among humans. When one looks about, one cannot help but notice the intense competition between men: between a man and his co-workers, between one family and another, among nations, and even among races. A very familiar example is the dominance relationship existing between parents and their children, or between siblings[9] of different ages. The competition may be for subtle goals and involve only status or psychological gain, or may be very intense and involve the economic necessities of life. The result of such competition is the domination of one individual, family, nation or race over others, much in the same fashion as a Cichlid fish competes with his neighbours for survival, or a group of howler monkeys competes with neighbouring groups for an adequate territory in which to live.

HISTORICAL NOTES

1878

The idea that no living being exists completely alone was first proposed in modern literature by ESPINAS. His great mass of observational data led him to conclude that some sort of communal or social life is the rule, rather than the exception, among animals.

1922

SCHJELDERUP-EBBE observed the relationships among individuals in a small group of domestic hens. By examining the outcomes of fights over a period of time, he discovered remarkable consistencies in pair-relationships within the group. One bird characteristically won fights with each of the others, while another habitually lost to all of the others. Between the extremes, the members of the flock were arranged in a hierarchy of social status.

1952

ALLEE reviewed and summarized the results of his and his pupils' experimental observations on social dominance covering a period of more than twenty years. His findings, together with those of other investigators working during the same period, are integrated to formulate the phylogetic and ecological principles underlying the phenomenon of social hierarchy.

1953

The pertinent information on social hierarchies and aggression in domestic fowl was assembled by GUHL with a view to the practical application of biological principles. Thus, common management practices in animal and poultry husbandry, which had hitherto been largely based on empirical trial-and-error methods, were now placed on a firm scientific basis.

1960

Present investigations are directed towards clarifying the fundamental biological mechanisms which are involved in social hierarchies. The role of early social experience, the direct and indirect effects of hormones, the adaptability of evolved behaviour patterns, and so forth, are problems basic to behaviour in general; from such studies will arise a more complete understanding of the phylogeny and ontogeny of behaviour, and therefore of social hierarchies.

The language of bees

Martin LINDAUER

> *Anyone who troubles to watch the behaviour of bees will soon realise that they must have a means of communication between themselves. It may be days before bees notice a pot of honey left uncovered. But, as soon as one bee discovers it, dozens, then hundreds of her hive companions rush to the booty. Somehow, the first bee has told the story of her find and the news has spread throughout the hive.*
>
> VON FRISCH

In order to survive, animals must be able to communicate with one another. The male has to inform the female that he belongs to the same species and is ready to copulate, and the young must be able to ask their parents for food. Usually these signals are very simple: a gesture, a cry, a movement, or a special scent carries the primitive message. Animals which live in herds, such as roedeer and chamois, require rather more elaborate methods of communication: an alarm to warn the herd of danger and a pattern of scent markers which enable the scattered individuals to reunite when the crisis is over.

Some years ago, a German scientist, Karl von Frisch, made the important discovery that bees communicated in a much more elaborate way, by means of what he called their 'language' because in many respects it resembles the complexities of human language. The bees' language enables them to pass on messages of sufficient complexity for the recipient to act on the information he has received and set off, for example, on a particular line of activity.

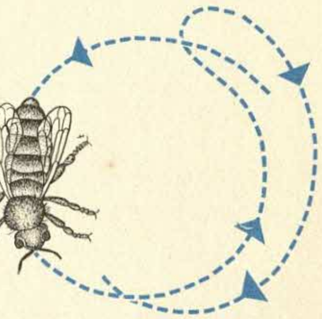
However, the language of bees is very different from human language. First of all, there is the physical difference because, whilst we communicate for the most part by sound, the bees do so by a combination of the senses of smell, feeling, and pressure. Secondly, and even more important, there is a psychological difference. Bees are unable to form abstract concepts—a fact which has been discovered, not so much by an examination of the language in itself, as by observation of the behaviour of the insect employing it.

A call for reinforcements

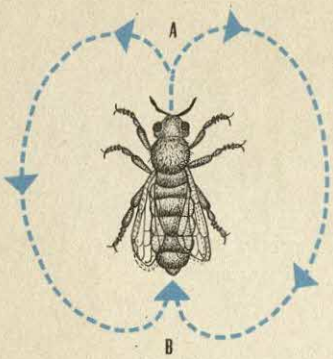
In any hive, only a proportion of the bees are fully active. At one time it was thought that only the males or drones were lazy, but closer examination has shown that all the bees spend a considerable part of their time walking about in the hive, or simply doing nothing at all. This discovery was made by marking a few thousand bees individually and measuring with a stop-watch the amount of time spent in various activities.

These idle bees, in fact, play an important part in the life of the hive: they are the strategic reserve ready to go to work at a moment's notice if one of the experienced honey gatherers comes back from an exploratory trip with reports of a good find. The explorer requires auxiliaries to help her gather the harvest of nectar and pollen because flowers close quickly and there is always the fear that a competitor will arrive on the scene before the discovery is exploited. On these occasions the bees' elaborate mobilisation system comes into action.

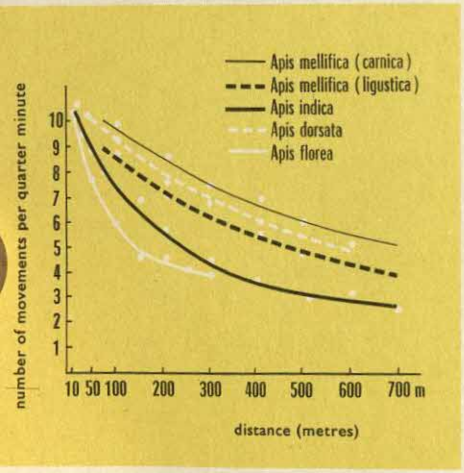
The explorer bee, when she has located a rich source of food-material, returns quickly to



A bee which has found food close to the hive performs a circular dance in order to alert the worker bees and persuade them to go out and collect it.



When the bee wants to inform the workers of a distant feeding-place, she performs a more complicated 'wriggling' dance. During the straight-line part of the dance, from B to A, the bee wriggles her body. The frequency of the wriggles indicates the distance of the food find.



The languages of different species of bees differ in the way they indicate distance. In this graph the vertical axis gives the number of wriggles in fifteen seconds during the wriggling dance, and the horizontal axis the distance of the food find. The honey bee Apis mellifica *makes nine wriggles in fifteen seconds to indicate a distance of 600 feet, while the Indian dwarf bee* Apis florea *makes only four wriggles to give the same message.*

the hive, distributes some of the food close to the entrance and rouses the unemployed bees that she meets. The news is spread without any vocal sound, since bees are deaf, but by a peculiar dance. The explorer excitedly begins to make half-circles, sometimes to the right, sometimes to the left, while trying to touch the bees around her. These in turn, are aroused and try to follow the dance figure, sometimes as many as six following the explorer, holding each other closely by the antennae, almost as though they were dancing a conga. Closer inspection of the dance shows that those bees which have understood the message correctly fly off and discover the source of food in the least possible time: they have followed the explorer's communication well enough to fly straight to the find.

It might be thought that the worker bees, stimulated by the dance, simply follow the explorer back to the food. But this is not the case. Experiments have been carried out with artificial food sources and a marked explorer, which show that the workers are able to find their own way to the food without being accompanied by the explorer. How do they do it? The only possible answer is that the information needed to discover the food must be related to the details of the dance performance.

The circular dance

The experiments of von Frisch have clarified the method by which the workers learn where to find the food. In the simpler cases the explorer bee, on her return, performs a circular dance; in one experiment a small cup of syrup perfumed with two drops of essence of lavender, was placed ninety feet from the hive entrance. The first worker bee to discover this windfall returned to the hive and performed her circular dance, which conveys to the other workers in the hive three pieces of information: first, that a find has been made which requires to be harvested; secondly, that it is close at hand; and thirdly, that it smells of lavender. This latter message is conveyed to the bees who follow the dance when their antennae touch the lavender-scented fur of the explorer. The experiment can be extended to show that this is precisely the extent of the information passed. When a series of cups, without syrup, but some scented with lavender and some with peppermint were placed fifty yards or more from the hive, in addition to the syrup-filled cup, the worker bees visited the lavender-scented cups rather than the syrup-filled one and only those which were nearest to the hive. Scented cups placed more than a hundred yards from the hive entrance were not visited.

Obviously, the circular dance gives quite precise information. It corresponds roughly, in human language to the statement: 'Wake up and help to harvest some nectar I've found. It's not far away and smells of lavender'.

The wriggling dance

The experiment was then extended by placing the syrup-filled cup at greater distances from the hive, up to about 550–600 yards. The worker bees found the cup, even at this distance, as easily as they did before. If, after the explorer bee has discovered the syrup at 550 yards, the cup is quickly moved in to 50 yards before the worker bees have set out, they miss it completely. They are looking for a find at 550 yards.

The experiment can be made to yield still more information by placing additional cups in different directions and at different distances from the hive. The results are interesting. If the principal cup, the one discovered by the explorer, is 550 yards from the hive, additional cups placed nearer to or further from the hive are not visited by the workers. Similarly, if a whole series of cups is arranged around the hive at the same distance, the worker bees still go only to the one which was discovered by the explorer. In other words, the worker bees know both the direction and the distance of the place described by the explorer.

The experiment has been repeated with the syrup cup at distances of five or more miles from the hive. It has been tested in many different regions, open countryside and forest land, and the results are always the same. The worker bees, informed by the explorer, always find the lavender-scented syrup, wherever we may put it.

Let us examine exactly what this means. A worker bee exploring four miles from the hive stumbles on a pot of syrup and alerts the others in the darkness of the hive with the information, but of course she has no map to show the workers where they should go nor have they compasses or measuring chains to aid their navigation. Yet within minutes they are at the exact spot where the syrup has been found. Again, all the information has been passed on by the pattern of a dance performed in the darkness of the hive. When the discovery is made at a distance the simple circular dance described above is modified, and between the alternate circlings, first in one direction and then in the other, an extra figure is added, a straight-line walk accompanied by 'wriggling'. This is known as the 'wriggle dance'. By observing the dancing bees closely it is evident that the rhythm of the dance varies according to the distance of the find and that the direction of the straight-line walk varies according to the direction in which it is to be found. No other information is needed. The explorer does not describe the place or the country over which the others must fly; for distance and direction are the only clues although the smell of the food doubtless helps them to locate it once they are in the right area.

The exact language of the wriggling dance can be translated by observing the bees when an explorer returns after finding one of the syrup cups. The faster the wriggling motion, the nearer the source of food: ten wriggles in fifteen seconds means food just over a hundred yards away; six wriggles in fifteen seconds, 550-600 yards; four wriggles, over half a mile; and two wriggles, nearly four miles. Information on the direction in which the syrup cup is situated is more difficult to appreciate; it is given by the angle between the vertical and the direction in which the wriggling dance is performed in relation to the sun. If the direction of the dance is vertically upwards, the goal is in the direction of the sun; if downwards the food is away from the sun and the workers must fly out with the sun on their backs. If the direction of the dance is 60° away from vertical to the left, the food is 60° to the left of the sun. The workers are given in the dance the angle at which they must fly in relation to the sun, and this is indicated by the angle between the wriggling dance and the vertical.

How bees orientate themselves

Now this means that bees, unable to see in the darkness of the hive, are capable of receiving precise directional information through well-developed organs sensitive to gravitation which, enable them to appreciate the angle between the direction of the dance and the perpendicular, and then, when they reach the entrance hole, translate this into optical co-ordinates to show the course they must fly with respect to the sun. The fact that they are able to do so implies sensory co-ordination of an accuracy which had not previously been observed in the animal world.

There are still many unsolved problems connected with the worker bees' ability to go directly to the syrup cup. How, for example, does it measure, to within a few yards, the distance it has flown from the hive? The flight may not always be in a straight line, for the bee may have to make diversions around buildings, and there may be strong head or side winds to upset navigational calculations. How, for that matter, does the worker bee correct its course for the effect of wind? For if the wind is blowing across its path, the course it must steer to reach the syrup cup will be different from that which it was given in the hive.

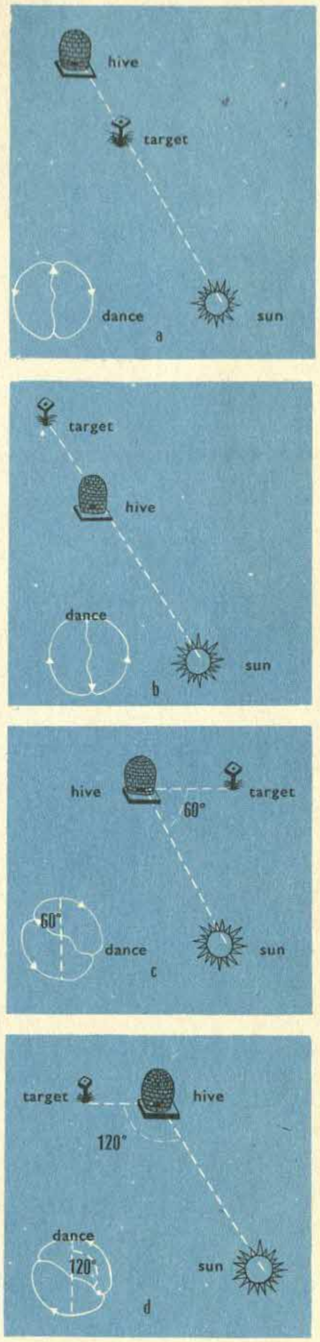
One mystery, at least, has now been solved. The worker bees find their way to the syrup pot even when the sun is obscured by cloud or has disappeared behind mountains. How do they sense the position of the sun and fly the appropriate course, even when it is invisible? The answer is that their eyes are capable of distinguishing the plane of polarisation of the light from any patch of blue sky, and this light, scattered by the molecules in the upper atmosphere, is invariably polarised in a direction depending on the position of the sun. In this way the bee knows exactly the direction in which the sun lies even though it may be unable to see it.

Having unravelled the language of the bees, we must ask ourselves a series of questions: Are bees unique, or do other animals have similar means of communication? Are some elements in the bees' dance of general use? Do primitive bees have less well-developed language than the honey bee? These questions are of interest to those who study linguistics as well as to zoologists, and may well throw light on the development of our own language; for it is usually supposed that the languages of animals differ from those of human beings in that they have no historical development and are used in the same way by all animals of the same species in every part of the globe with only small local and individual variations.

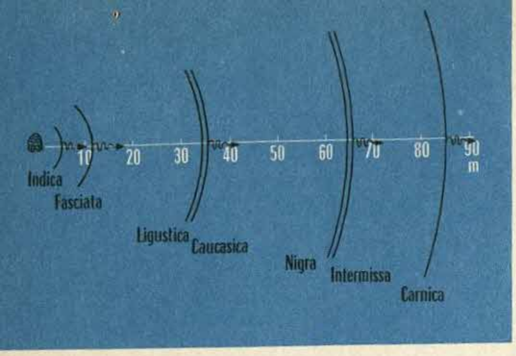
I believe that this view is incorrect, and wish to show, firstly, that the language of bees has evolved and developed over a long period, and secondly, that even among closely related colonies, it varies very widely indeed.

Dialects of the dance

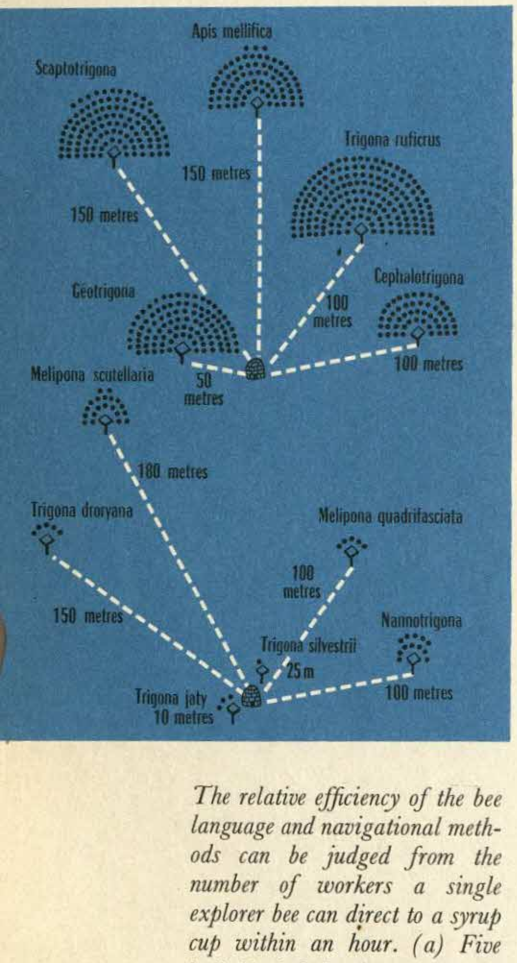
All the different races of bees, Italian, Caucasian, German, Egyptian and so on, use the same pattern of dances: the circular dance and the wriggling dance. But close observation shows that the details of the dance are not quite the same and the bees have different 'dialects' according to the region from which they come. For instance, a wriggling dance which an Egyptian bee would interpret as meaning food at 500 yards, would be taken to



The way in which the wriggling dance of the explorer bee shows the direction in which food is to be found: (a) wriggling dance directed upwards means food to be found in direction of the sun; (b) wriggling dance directed downwards means food to be found in a direction opposite to the sun; (c) dance at 60° to the left of vertical tells the workers to set course at 60° to the left of the direction of the sun to find the food; (d) dance at 120° to the right of vertical tells them to set course at 120° to the right of the sun.



The distance at which the simple circular 'rousing' dance is supplemented by the wriggling dance depends on the race of bee. To the left of the black lines, bees of the named race use a simple circular dance, and to the right, the full procedure with wriggling dance.



The relative efficiency of the bee language and navigational methods can be judged from the number of workers a single explorer bee can direct to a syrup cup within an hour. (a) Five individuals belonging to different species visited the syrup cup and the black dots show the number of workers who succeeded in finding it within an hour; (b) peated with other species less successful in communicating. In the cases of Trigona silvestris *and* Trigona jaty *only two or three bees found the cup, even at short distance.*

mean food almost a mile away by an Austrian bee: in other words, the wriggling rhythm of the Egyptians is much slower than that of the Austrian. If bees from different regions are put together in the same colony, they are unable to understand one another. For instance, marked German and Italian bees were put together in a hive, and an explorer of the German species discovered a syrup cup 130 yards from the entrance of the hive, upon which the German worker bees went directly to the cup. But the Italian ones went to the wrong place, for they had interpreted the German explorer's dance as meaning food at 110 yards. Other differences have also been discovered between the languages of the bees from different regions.

All these bees were, of course, of the same species, *Apis mellifica*, and even greater differences might be expected between the languages of other species of bee. The three main species, apart from *Apis mellifica*, are *Apis indica*, the Indian bee, *Apis florea* or dwarf bee, and *Apis dorsata*, the giant bee.

The Indian bee, which is the most closely related to the honey bee, and is sometimes raised in hives, has a dance language similar to the honey bee but with greater differences than the 'dialects' I have just described. The honey bee gives no indication in its dance of the distance or direction in which the food supply lies if it is less than about a hundred yards away; for these short distances the explorer simply performs a circular dance, saying in effect, 'Come on, there's food nearby'. The exact distance at which this simple message gives way to full directions varies a little between bees from different regions. But the Indian bee carries out the full performance, including the wriggling dance which gives direction and distance, for any find more than two yards from the hive entrance.

In reporting direction, the system of the dwarf bee is much more primitive. These bees build their nests suspended from the branch of a tree and the workers congregate on the flat horizontal top of the nest and the dance is performed there. The explorer leads the workers by performing the wriggling dance in a direction pointing directly towards the source of food. The workers thus have a much simpler task, for all they need do is to fly in the direction they faced during the wriggling dance, and this they can fix in relation to the sun. Here then, is one of the most primitive forms of the bee language as we know it. It is effective, yet does not demand the complex process of interpreting the message passed by the sense of gravity in the dark interior of the hive, into a course to be steered with respect to the sun.

Bees on the trail

But an even more primitive language exists among some of the more distant relatives of the honey bee, such as *Melipona* and *Trigona*, the stingless bees. They have something in common with the honey bee in that they live in colonies and collect nectar and pollen. But their method of bringing workers to a source of food is much less efficient; in an hour, only two or three workers of some of these species, such as *Trigona ruficus*, are able to find their way to a syrup cup, compared with hundreds of honey bees.

This species has a crude but reasonably efficient method of mobilising workers to collect food. There is no dance like that of the honey bees, but the explorer bustles around the hive bumping into workers to excite them. She then sends a group of workers from the hive and they explore in gradually increasing circles until the treasure is found. The only important piece of information conveyed to the workers by the explorer is the scent of the food and this helps them to reach their goal.

Some of the stingless bees have developed quite a different method of reaching the explorer's find. On the way back to the hive the explorer bee lays a trail by depositing from time to time a droplet of scent along the route she is flying. The workers then follow this trail, like a paper chase. The method is not as highly organized as the translation from one sense to another of the honey bee.

The analysis of the bees' language shows to what a remarkable extent social co-operation can exist in an insect community. It is such a highly organised method of communication that it would be surprising to find it in many of the higher animals, let alone the relatively lowly insects.

Animal thought

Otto KOEHLER

It is now a century since Darwin published his theory of evolution, a hundred years during which, in spite of the resistance of some laymen to the idea, all biologists have come to accept that Man evolved from the same ancestors as the animals.

However, the pattern of evolution is clear. Man evolved from Primate ancestors by processes which are much better understood today than when Darwin first put forward his theory; for it is evident that human beings emerged as a result of a series of mutations, Mendelian re-combinations, and the powerful forces of natural selection provided by the environment, and to this progressive evolutionary development man owes the whole of his hereditary wealth which determines the limits of the evolutionary possibilities of his behaviour. Gradually, through the acceptance of this concept, a link has been forged between the psychologists, concerned with human behaviour, and the ethologists, such as Konrad Lorenz, who study animal behaviour.

The higher animals share the same sensory stimuli as man and some of them have developed certain senses, such as smell and hearing, to a higher degree than mankind. They also share many features of physiology, as is shown in the successful application of the results of animal experiments to human medical problems. This similarity extends to the ganglion cells, and the nervous systems of fish, frogs, rabbits, cats and dogs.

Ethologists are frequently concerned with the study of the innate behaviour of animals, that is, behaviour which is known by instinct and does not need to be taught. Thus, a foal does not need to learn how to walk, trot, or gallop; a bird does not have to learn how to fly; nor a human baby how to clamber on his mother's breast. As Peiper has demonstrated in a film, a newly-born baby, when supported by the head, can swim like a dog, walk, and even go up and down stairs. It is not inconceivable that some human beings may have an innate ability to navigate. The god-king Kon-tiki, for all that we know, was able to reach Easter Island presumably without the help of compass, sextant or chronometer, and 135 years ago Carl Ernst von Baer suggested that the fishermen of the Barents Sea then made use of a similar innate navigational ability; but these accomplishments do not compare with the exploits of eels, salmon, migratory birds, whales and seals. Similarly, the wide range of movements and mimes which animals employ in order to threaten, fight, salute, court, copulate, tend their young, and find food, is inborn and instinctive, and so are the inner motives which make them move on to new surroundings, as when birds migrate.

Innate releasing mechanisms

Such instinctive behaviour is expressed by a series of fixed action patterns: an inherited framework of actions which enables the animal to recognise a sexual partner, choose material for the construction of a nest, or raise its young. A ground-nesting bird knows that it must not look for a place for its nest on a tree or a chimney, which is what the stork does, only nesting on the ground as a last resort if its wings have been clipped. But the fixed action pattern is only aroused if the animal receives the correct stimuli or releasers known as innate releasing mechanisms.[1]

A mechanism of this kind ensures that the fixed action pattern of instinctive behaviour is only released when conditions are favourable. In our own language we use words like 'husband' and 'home' as releasers. They are 'concepts', and it has been claimed of a concept that it is linked to the word because it was originally created by the word. This relationship between a word and its meaning as a concept may occur in civilized man. For instance, when we first come across the word DDT, we learn something of its significance: its use as an insecticide, perhaps its chemical formula, or where to buy it, we get an impression of what it looks like, its colour, feel and smell, and all this information is added up to give meaning to the word DDT. Contrast, on the other hand, this wealth of meaning with the outlook of the man who actually invented the insecticide. He simply sought to synthesize a chemical which would kill insects. Only when he succeeded was he ready to give the new chemical a name.

When a male bird has chosen a territory

Parrots are remarkable subjects for experiment; they are capable of complex procedures which confirm the evidence that has been collected on the existence of unformulated thought. (Photo Lod).

The highly evolved monkeys (see opposite page) are able to associate a number of objects in order to attain a goal. Their behaviour shows them to be capable of simple reasoning on which their actions are based, but they remain incapable of formulating their ideas. (Photo Lod).

and a mate, this particular territory and this particular mate take on a special significance: he learns to recognise their specific characteristics and incorporates them into the framework of his fixed action patterns. They become for him, an unformulated concept, individualised and personified. Human beings use proper nouns to express concepts of this type. Our bird takes his companion to the nest, takes turns at sitting on the eggs, and chases away other female birds which may encroach. This involves judgement. In effect the bird has decided: 'This female is mine, that one is not.'

Another example: a fish is aggressive within the limits of the territory that it recognises as its own, but when passing through another territory it becomes afraid and leaves it as quickly as possible. The fish acquires remarkably detailed information about its own territory. For instance, a fish has been observed to retrace a trail fifteen yards long which had been learned in the course of a few hours during the night at high tide, and was even able to negotiate it at low tide when there was little water and numerous dry sand-banks. In so doing, the fish had to make a series of unformulated judgements before swimming or jumping from one puddle to the next. Expressed in words, he must have decided: 'Here I must jump to a certain height and in a certain direction, otherwise I am lost.' Or again, when he met another fish, the decision had to be made: 'I am at home here, so I shall chase away this intruder'.

All the instinctive social expressive movements of animals are instinctively understood by their kind. The domestic honey bee,[2] for example, performs an instinctive wriggling dance in order to convey to her hive mates the location, in distance and direction, of a source of food and this dance is perfectly understood by the workers which become involved in it, and then set out from the hive and fly directly to the place indicated. Unlike the human child, the young bee does not have to learn the language of its elders.

Unformulated thought

Anyone searching for something with no idea where it is to be found, is likely to take a long time about it, unless he is exceptionally lucky. The process is one of trial and error and when an error has been made, another possible hiding place is tried. But suppose the search is of a type which is conducted habitually, for instance in the case of a customs officer searching for contraband. Here the searchers often appear to be uncannily accurate; for experience of previous searches has enabled them to build up a store of knowledge about the likely places in which contraband may be hidden; the method used is one of trial and success.

This latter process involves a degree of unexpressed mental activity in which reasoning processes are carried out without being precisely formulated. Wolfgang Köhler has called 'primary solution' an animal's trial using its head rather than its hands. He hung a banana from the ceiling out of reach of a chimpanzee. The chimp found a box, dragged it across the floor until it was underneath the banana, climbed onto it, and took the fruit. In another case, the banana was placed near the bars of the chimpanzee's cage, but too far away to be reached by its arms. This time the animal climbed a tree, broke off a branch, and used it to draw in the fruit. In both cases an unexpressed mental process was involved. A man who has no hammer to knock in a nail may take off his shoe and use that. He sees the shoe in relation to his concept of a hammer; the chimpanzee 'conceives' the stick as being related to a branch.

Neither man nor monkey formulated these thoughts: the only difference between them is that the man *could*, if he chose, put into words and express to other people the methods he had employed. Children, before they have learned to talk, behave just like animals and have a whole repertory of nouns, concepts, and judgements, which remain unformulated, and quite often, after a child has learned to talk, it will describe an event which happened before he could express himself. The young child gradually attaches words, learned from adults, to his own unformulated concepts.

There are many other examples which show that we share mental processes with animals. For instance, von Helmholtz thought that optical illusions were errors of judgement but we know now that fish, hens and many other species are deceived as easily as we are by these optical tricks. Physiologists, such as Erich von Holst, together with psychologists are now trying to study them on a scientific basis. Rather similar effects are seen in what are known as 'constancy phenomena'; thus, although the image of a man on the retina of the eye becomes smaller as he moves farther away, the brain does not interpret this as meaning that the man is shrinking, but that he is far away, and the same is true of familiar shapes viewed from unfamiliar angles. Similarly, we recognise a melody whether it is played on a

---

(1) *See p. 75 for a chapter on 'Releasers'.*

(2) *See p. 87 for a chapter on 'The Language of Bees'.*

piccolo or a double-bass and regardless of key.

As animals are capable of abstraction based on sensory perceptions, which we are said to do only with the help of words, we must conclude, since this faculty is shared by man and animals, that we have inherited it from them. Indeed, it is not unreasonable to reverse the argument and go one step farther to assume that in the course of evolution this faculty of deduction may have been responsible for the development of a vocabulary, for the concept must be there before we feel the necessity to give it a name. If human language was created in this way, because man and man alone gave names to the thought elements inherited from animals, we have an answer to the philosophers' discussions on the 'pre-established harmony' between the natural event and its description in words; for according to this theory, the word is adapted to its usage, since each word denotes the unnamed element for which it was created.

Experiments on animal thought

The major objection to reasoning of this kind is that all the animal 'languages' that have been investigated prove to be examples of innate behaviour and everything animals might learn beyond this inherited language is limited by hereditary factors which, in turn, are determined by the normal requirements for survival in a given environment. For example, the information contained in the bee's wriggling dance, gives only the distance and direction of the latest food find. The explorer bee is unable to pass on one vital piece of information: height, because there is no 'word' for height in bee language. So while the bee's language is a two-dimensional one, it has to fly in a real world of three dimensions. However, since the range of heights at which nectar is to be found is rather limited, the two-dimensional language does not put bees at a serious disadvantage. Man, however, can express himself in three space dimensions and time and he can even manipulate mathematically in many-dimensional systems. So if we want to show how our faculties of expression originated and evolved, we must attempt to make animals solve problems which lie outside the experience of their normal wild life and should not then be criticised for doing unnatural experiments. In fact, all experiments are by their very nature unnatural.

Abstraction from sensory data

Dinger succeeded without difficulty in teaching mice how to get out of a fairly com-

plicated maze in which, at different points in the course, there were at first one-way doors, so that any mouse which passed through them was unable to return to the starting point. Another factor which helped the mice to discover the correct route was the droplets of urine excreted on the floor; as the animals became more skilled and larger numbers completed the course, the number of marker droplets increased and the number of mistakes became fewer. Again, the laboratory walls reflected the sounds produced by the mice in the maze, and this may have helped to orientate them and, finally, the noise or smell of mice in a cage in one corner of the room may have given those in the maze a fixed bearing.

Dinger then removed successively each of the four possible clues which his mice had been given. First, he removed the one-way doors. Then, after each attempt, he removed all traces of scent which had been left in the maze and finally, he rotated the maze through changing angles between each attempt, so that the effect of sound reflected from the laboratory walls or of noise from the other mice in the laboratory could not be used for direction-finding. After each clue had been removed, the mice again made many mistakes and lost their way in the maze, but they re-learned the way far more quickly than at first. After three months the mice had solved the problem perfectly, even when blinded, and were able to run straight through the maze without having any of the original clues to help them.

But they still retained one extremely important factor: their kinaesthetic sense, which concerns the habitudinal movements of the body which make their appearance after long practice and enables us to type, cycle, skate, or play the piano. Anyone who walks or drives over the same route every day acts in the same manner when what once had to be learned ends up by becoming automatic. Was this how the mice had become so skilled at finding their way out of the maze? Dinger eliminated this possibility by trying the skill of his mice in some modified labyrinths. The original maze had passages which intersected at right angles, so four new ones were built, each similar in pattern to the first, but with these differences: (1) had angles of 45° and 135° instead of 90°; (2) was identical with (1) but where this had 45° angles (2) had 135° angles and vice versa; (3) had 90° angles and was in all respects like the original maze on which the mice trained, except that all distances were doubled; (4) was a 90° labyrinth like the original one but, where that had a turn to the left, (4) had a turn to the right—a 'mirror image' of the original.

The raven, like the jackdaw, can be trained to count, but so far nobody has succeeded in teaching the bird to recognise more than six objects. (Photo Lod).

Dinger tried out a number of mice trained in the first type of labyrinth in the new ones, and found that they needed no re-training. Sometimes they would make mistakes over the first unfamiliar turning, but they soon 'understood' what had happened and completed the rest of the course with hardly a single error. The mice had, in fact, developed an idea of the total configuration and their ability to 'read' the labyrinth is comparable with our own ability to read a letter, print, or a map.

'Counting birds'

Another example is the case of the 'counting birds' which have been an object of our research for nearly forty years. Birds appear to have two separate arithmetical abilities: they can recognise numbers simultaneously, as we recognise at a glance the number of pips on a playing card; or they can count, for example, the sounds of a metronome.

The most simple 'simultaneous' experiment is carried out in the following manner: a piece of card is placed at right angles to the path along which a pigeon is moving, and at one end of the card we place two grains of wheat, at the other end three grains. We allow the pigeon to take the three grains, but if it attempts to take the two, it is frightened away. Sometimes the three grains are placed on one end of the card sometimes on the other, so that the side (left or right) bears no relationship to the number. Slowly, the pigeon learns to take the three grains every time.

In this way we have managed to teach pigeons, after much training, to distinguish between four and five: but it has never been possible to teach a pigeon to distinguish between five and six.

Jackdaws and parakeets were taught by a number of different methods to distinguish five from six with complete assurance; ravens, magpies, amazon parrots, a grey parrot, and a squirrel, were even able to distinguish six from seven. In further experiments, birds had to match samples rather than select a number. For example, they were presented with five containers covered with white lids on each of which were 3, 4, 5, 6, or 7 pips, whilst nearby lay a solitary lid known as the 'sample', on which the number of pips was changed at each trial. The problem for the birds was that only if they opened the container whose lid bore the same number of pips as the sample would they find food. They had therefore to learn to compare numbers.

The crows can learn, after long training, to count to seven. This is a considerably better performance than some primitive peoples can lay claim to. (Photo Lod, by permission of Professor Bösiger).

At the start of the experiments yellow drawing pins were used to mark the pips on the lids and the sample and the heads of the drawing pins were arranged in regular patterns like the pips on a domino, so that the birds were helped by the characteristic pattern. Later, this 'pattern clue' was removed, and the marks arranged in a random way.

Our raven Jacob, after having been trained with patterns, recognised immediately the same numbers in random arrangements. We changed the marking again so that, although the number of marks on the sample and the lid of the food container remained the same, the size and shape of the marks and their arrangement were very different. Again Jacob did well without re-training: he could now only solve the problem by counting, since all other clues had been removed.

How much aptitude have human beings for a test of this sort? We showed 100 slides to more than 200 subjects, in order to test their ability to distinguish the number of marks in a pattern corresponding to the last and most difficult task which Jacob solved: they had to match samples from three to seven with constantly changing sizes, shapes and arrangement of the marks. The patterns remained on the screen for a time which would have been long enough for Jacob to distinguish between them, but not so long that the human viewers had an opportunity to count them numerically in terms of words. None of the humans tested could surpass the best performances of the raven, squirrel, grey parrot or magpie. None did better than to distinguish a group containing seven dots, and many were on a level with the jackdaws and parakeets and reached only six. A few were on the same level as the pigeon and unable to distinguish numbers above five. In other words, we are no better than animals in the instant optical recognition of numbers if we are not allowed numerals.

Successive counting

But numbers can also be recognised in another way, when events occur successively. For example, if you are immersed in a book when a clock strikes, you may become aware of the time without consciously counting the strokes, although in this case there is an additional clue, since the regular rhythm of the strokes helps to reveal the number.

Animals possess this same faculty. In one of our experiments we offered a pigeon dried peas which fell from the end of a short tube into a circular cup where they rolled about like billiard balls. This particular pigeon was a little slow in his reactions, and sometimes had to make at least fourteen attempts before he succeeded in catching a pea as it fell. The peas were arranged to drop at random intervals spaced between one and sixty seconds, thereby removing any assistance which the bird might get from a regular rhythm. If the bird tried to peck every sixth pea that fell it was punished but was left alone after the other five. It quite soon learned the trick, and once the training was complete continued to ignore the sixth pea.

Other experiments have given even better results, and this in cases where no punishment was given when the bird made a mistake. A row of identical saucers with identical unmarked lids faced the bird which was trained to lift off the lids in succession one after the other to find the titbits they contained. At each trial exactly the same number of pieces of food were placed in the saucers, but the distribution was random. The bird could never know which saucer would be empty and which would contain a rich haul. Sometimes all the food might even be in one saucer. Faced with these circumstances it gradually learned how many pieces of food it could expect to find in the saucers, and when it had found the last of them did not trouble to look any further and would return to its cage without lifting the remaining lids.

A jackdaw was trained in this way to count up to five, and on one occasion the usual sort of problem was set for him. One titbit was placed in the first saucer, two in the second, one in the third, none in the fourth, one in the fifth, and none in the succeeding saucers. The jackdaw lifted the lid off the first saucer and took the offering, and did the same with the second and third. Having taken four pieces of food, it ignored the rest of the saucers

F EDUCATION
BANIPUR

S.C.E.R.T., West Bengal
Library
Calcutta
25/3, B. C. Road

and returned to its cage. Then at the very moment when the observer was writing in his notebook: 'Failed; animal took only four instead of five pieces', the bird returned to the saucers, lowered his beak once in front of the first saucer, twice in front of the second, once in front of the third, and then lifted the lid on the fourth saucer. Finding nothing there, he lifted the fifth saucer lid, took the food it contained, and returned once more to the cage without lifting the sixth or any other lid. The lowering of the beak in front of the saucers which had already been emptied was evidently a re-count of the movements made when it had missed the fifth and last piece of food. This decision to re-count was made without any hint of intervention.

The squirrel is also able to tackle difficult problems and has shown itself adept at transposition.

Problems of transposition

In order to recognise the number of objects in a group, we use our eyes. But we do not know of any sense organ which might be responsible for the counting of successive events. There seems to be no sensory link between the simultaneous perception of a number in a group of objects and the successive counting of objects which are revealed one at a time, except in the special case of man who has names for the numbers.

As soon as a small child can count aloud from one to six, he will understand without trouble or practice what he is expected to do when someone says: 'You can take as many pieces of cake from this plate as the number of fingers I hold up.' The experiment requires transposition between the simultaneous recognition of a number of objects in a group (the fingers) and the successive counting of objects (the pieces of cake taken from the plate). We can now set the child a rather different task, which again he can usually perform easily. By his plate we put a number of groups of dots, like simple playing cards, each group containing between one and six dots. The child is allowed to eat a number of cakes and the experimenter then says: 'Show me the card with the same number of dots on it as the number of pieces of cake you have eaten.' This time the transposition has been made in the opposite direction, since the successive counting (pieces of cake) came first and the child then recognised the card which matched it. Jackdaws, a squirrel, a raven, a magpie, and a grey parrot have solved similar problems.

Our animals have even been known to carry out transpositions much as Dinger's mice quickly found the correct route through a new maze by transfer of their experience of the original one. For example, a jackdaw had learned to lift a lid marked with three spots and not to touch one marked with four, and one day, without any preparatory training, we presented it with a new situation. Instead of the marked lids, we used plain lids, placing three live mealworms on one and four on the other. The bird did not lift the lids, but ate the three mealworms and left the four on the other lid untouched. P. Lögler, in the case of a grey parrot, has observed no less than fifteen transpositions of this sort, many of them much more complex. For instance, he was able to teach it to take two seeds from a series of saucers when he flashed a lamp twice, but to take three when he flashed the lamp three times. In this case the transposition was from the perception of successive stimuli (the flashes of light) to the performance of successive tasks (the taking of the seeds). At a given moment during the experiment the flashing light was replaced by sound signals of adjustable pitch and loudness which could be made to follow each other at any required interval. The parrot solved the problem at the first attempt, realising that it was now required to behave with sound signals in the same way as it had done with the flashing light: it had succeeded in transposing, without additional learning, from a visual stimulus (the light) to an acoustic one.

In another case the same parrot was able to make a spontaneous transposition at the first attempt and with no extra training from successive counting to simultaneous or group counting. Cases like this have nothing to do with the qualities of the experimenter, but only with those of the animal subject. They demonstrate, in a particularly striking way, that animals are capable of 'intelligent' thought, although they cannot express it verbally.

Of course, I am not suggesting that parrots or ravens will some day become men. But our experiments do show how much of the special faculty that has long been regarded as the prerogative of man alone we owe to inheritance from the animals. The animal's unformulated thought is an essential first step towards the birth of human language which, of course, distinguishes us from them. If the marvel whereby man evolved from the animals is still little understood, it is re-enacted every day in the nurseries of our children: they are born as small animals without a language, then one day they begin to babble odd sounds, the next to imitate, and shortly they are talking and for many years to come will continue to extend their vocabulary and use of language.

Curiosity in animals

Robert A. BUTLER

Curiosity seems to be the basis for a great deal of man's behaviour. Man is inquisitive and the acquisition of new information is undoubtedly a self-rewarding event. His curiosity is probably most clearly expressed in the behaviour of young children.

During the first two years of life the child engages in an enormous amount of exploratory behaviour. New sights and sounds are usually pleasant events and he acts to promote these novel experiences. Obviously, by manipulating objects in his surroundings and perceiving the consequences of his acts, the child gathers a vast array of facts about his world and it is quite possible that the endeavours of artists, writers, and scientists, represent a continuation of these exploratory tendencies manifested so early in life. One may go so far as to suggest that curiosity is, in part, responsible for man's exalted station in the animal kingdom.

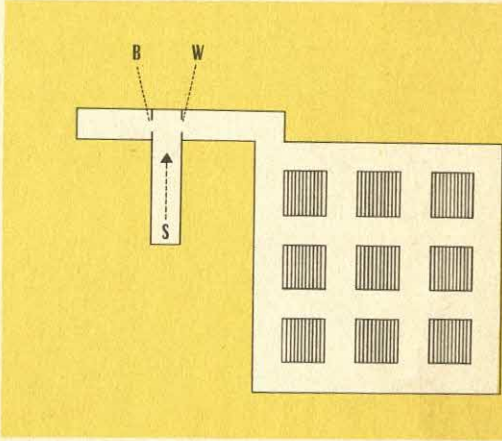
If curiosity is, indeed, such an important motive in man, should not there exist some semblance of curiosity-like behaviour in lower animals? In the light of the close biological relationship between man and other animals, it is difficult to conceive of curiosity as emerging only at the human level. Furthermore, there is much to be gained by beginning with lower animals when studying curiosity since their previous experience, in addition to the general testing conditions, are subject to much greater experimental control. As it turns out, many different animals can be used to investigate curiosity experimentally, and monkeys are admirably suited for this type of programme. They spend a large amount of time visually exploring their environment; they appear to be most attentive to various sounds; and they manipulate and examine carefully almost any new object that is presented to them.

In order to demonstrate the presence of curiosity in monkeys experimentally, one must show that the opportunity to engage in new or different experiences can serve as incentives for behaviour. If this can be done successfully and consistently, then we may, with reasonable assurance, infer that curiosity is an important motivational mechanism. Many experiments relevant to this issue have been conducted on monkeys within the last few years, and the great difference between these studies and traditional research on animal behaviour lies in the techniques employed to reward behaviour. Instead of using food, water, sex, or escape from pain to reinforce the desired response from the animal, these experiments utilise those rewards inherent in the experience of seeing, hearing and manipulating.

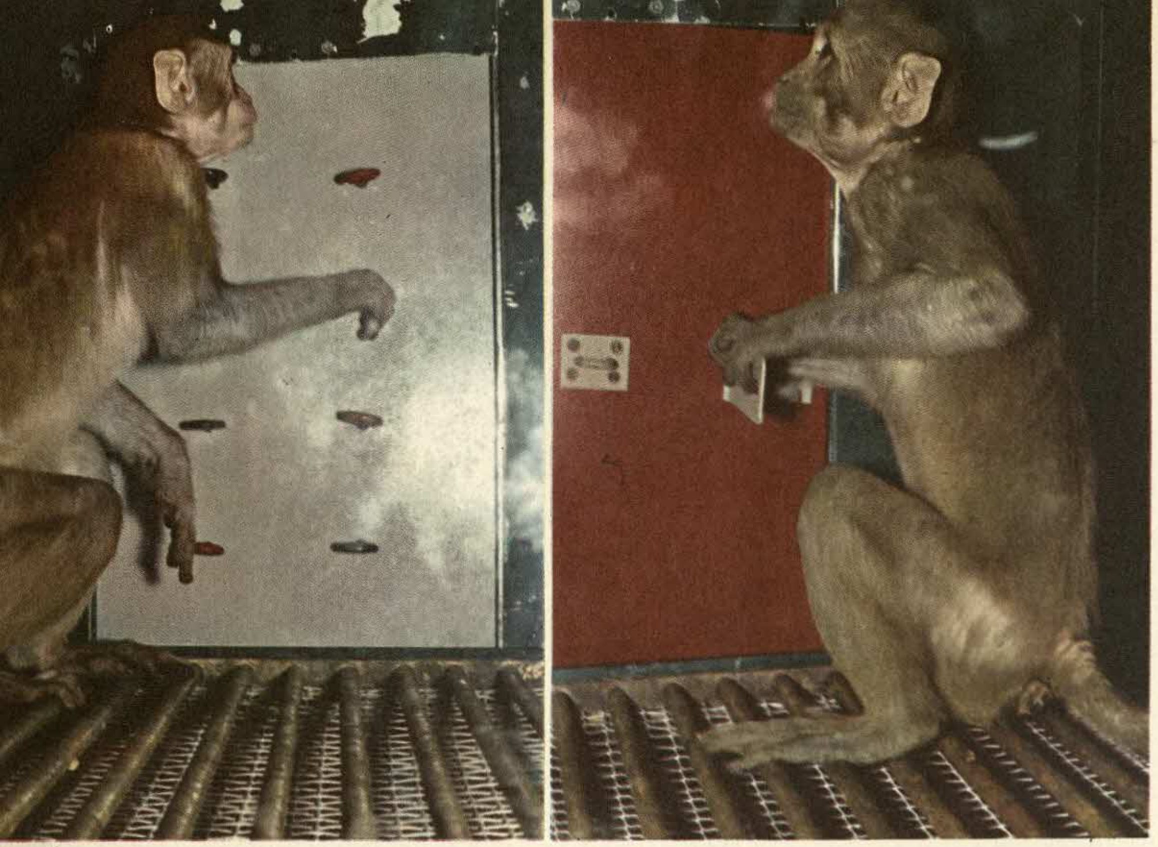
The pleasure of discovery

Professor Harry F. Harlow was among the first to emphasise the importance of this class of incentives for animal behaviour and the early experimental work was carried out in his laboratory in 1953. In the original experiment, rhesus monkeys were presented with a three-part mechanical puzzle the solution to which consisted in first lifting a pin, then moving a hook to one side, and finally raising a latch, an error being defined as touching any of the puzzle devices out of sequence. Monkeys learned to solve this problem with no rewards other than those intrinsic to the act of manipulating the puzzle devices, and Harlow and his associates went on to show that they could solve even more complicated puzzles. Equally important was the finding that monkeys will continue to work at manipulating the puzzle for many consecutive hours so long as someone is around to reset it periodically.

A later study demonstrated that monkeys were capable of learning colour discrimination problems for manipulative rewards. In this situation, a monkey was presented with a board containing several pairs of screw-eyes and, whereas all of them were inserted in the board, some were removable while others were not. The only clue as to whether a screw-eye could be removed was its colour. For example, in a red-green colour discrimination problem, the red member of the pair could be taken out, but the green screw-eye would be firmly attached to the board. A correct response was defined as touching the red screw-eye and an error was recorded if the monkey touched the green one. After a few test sessions, the monkeys reached only for the red objects, although the only apparent reward for learning this and other similar problems was the privilege of handling, inspecting, and in general, playing with the removable screw-eyes.



T-maze with secondary complex maze to test the curiosity of the rat. S: starting point, B: black door, W: white door. It is possible to change the doors around and the maze goal is capable of being attached to either branch of the T. (After Montgomery and Segall).



Monkeys undergoing a colour-selection test. By this means we can demonstrate that the satisfaction of manipulating an object constitutes a sufficient motive in itself for solving the problem.

The manipulative propensities of chimpanzees have also been subjected to experimental investigation. These chimpanzee studies conducted by Welker were designed primarily to demonstrate the importance of novelty in eliciting manipulative and investigative behaviour. The animals were exposed to several pairs of objects, but only one pair was presented during a single observation session and each member of the pair differed from the other with respect to either size, form, colour, brightness, texture, or moveability. The frequency of manipulating the objects and the time spent visually inspecting them were recorded. As with observations on young children, the chimpanzee would become bored if the same pair of objects was presented over and over again, but if new objects were introduced periodically, manipulation, accompanied by visual inspection of the objects could be maintained at a reasonably high level. Another interesting finding was that the younger chimpanzee of three to four years, engaged in more manipulative behaviour than the older animals of seven to eight years.

Visual curiosity

It seems quite clear from these experiments that manipulative activity in the monkey is a self-rewarding event. The chief importance of the chimpanzee studies is that they attest to the importance of novelty as an effective arouser for curiosity.

Monkeys almost continually watch what goes on in their surroundings and perhaps their visual attentiveness is one of the main reasons why monkeys enjoy such popularity at the zoo: there is an extremely close visual interaction between the observer and the observed and one wonders whether man or monkey gains the most from the experience. After working with rhesus monkeys in a variety of situations, it becomes apparent that these animals will go to great lengths for the opportunity to see what is happening outside their vicinity and such observations provide a clue as to how to investigate the visual exploratory behaviour in monkeys experimentally. The actual testing conditions are simple. A monkey is placed in an enclosed box and it is required to perform a simple task in order to gain visual access to the world outside the box.

The first experiment in a series of studies by Butler was designed to find out whether monkeys would learn a colour discrimination problem for visual reward. The monkeys were placed in an enclosed box located in a large room where many of the laboratory workers and visitors usually gathered and on the front of the box were two small doors through which the monkey could watch the activities within the room. A blue card was attached to the inside face of one door and a yellow card was attached to the other. These cards could be switched easily from door to door. For each test trial, both doors were closed, but the door holding the blue card was always unlocked and the door holding the yellow card was always locked. If the monkey pushed against the door supporting the blue card, the door opened and the animal was permitted to view the proceedings within the room for thirty seconds. If the monkey pushed against the door supporting the yellow card, a small light located on the outside of the box was activated, thus signifying that the animal had made an incorrect response. Monkeys rapidly learned to push only against the door holding the blue card. Several other colour discrimination problems were presented and the monkeys performed each one proficiently.

Another question immediately arises. Will monkeys work persistently for visual rewards? This question is important for, if curiosity is a primary motive for monkey behaviour, responses to curiosity-arousing events should be maintained throughout prolonged and repetitive test sessions. As might be expected, the responsiveness of monkeys to visual rewards depends upon what they are permitted to see once they have pushed open the door. For example, in one experiment, monkeys were placed in a box containing only one door.

Upon opening the door, the animal could view an enclosed room. On some days the chamber was empty but on others it contained either an array of palatable food, an electric train working, or another monkey. Monkeys opened the door much more frequently when either the electric train or the monkey was present in the room. A view of food produced no more door openings than did a view of the room when empty.

The sight of a colony is a potent motive

Probably the most exciting and interesting visual incentive for a monkey is a view of a monkey colony. Monkeys were tested under this incentive condition ten hours a day for six consecutive days. They were allowed to open the door as frequently as they wished and they could hold the door open for as long as they desired, but as soon as they released the door a spring would immediately close it. Frequency of door-openings and the length of time that the door was held open were recorded automatically. The results were dramatic. Monkeys spent nearly half of the total test time of sixty hours viewing the activities of the monkey colony. Furthermore, they engaged in as much observation on the last test day as on the first.

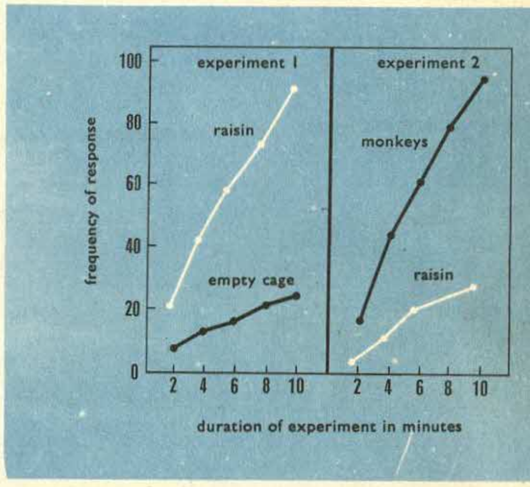
One feature should be emphasised at this point. These data demonstrate that a view of other monkeys serves as a strong visual incentive. But even in this situation, the performances of monkeys are not indiscriminate. It makes a difference to the test animal which particular monkey it is permitted to watch, for monkeys will spend more time looking at one animal rather than at another. In some experimental sessions, there were two windows in the test box. If the monkey being tested goes to one window he sees his cage-mate and if he goes to the opposite window he sees one of several other monkeys. Under these circumstances, the test animal usually prefers the window that lets him see his cage-mate.

In fact, testing conditions can be arranged so that a monkey would rather look than eat. The following situation illustrates this point: A monkey going to window A sees his cage-mate housed together with a monkey of the opposite sex. Upon going to window B he receives a raisin. Some monkeys will approach the window that provides the visual experience significantly more times than they will approach the window associated with food reward. The number of times that the monkey goes to a window for raisins is compared to the number of times it goes to the opposite window for a view of an empty cage, and a comparison is made between response-frequency for raisins with response-frequency for a view of other monkeys. The factors underlying these complex social relationships need to be worked out in much greater detail. The fact remains that a view of certain social situations can be a most compelling experience for a monkey.

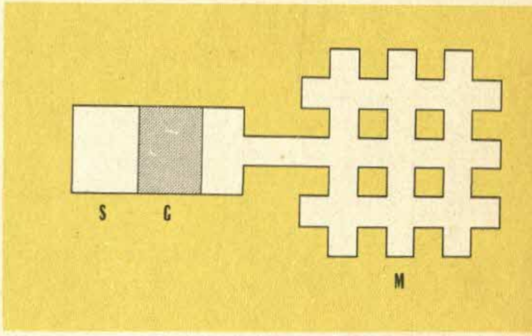
If there is little or nothing to see, monkeys stop opening doors or looking out of windows. The most effective way to extinguish viewing behaviour is simply by making the room outside the test box totally dark when the monkeys will very soon cease to approach the window. Observing behaviour can easily be reinstated in the next test session, however, if something is present for the animal to see.

Frustration intensifies the exploratory drive

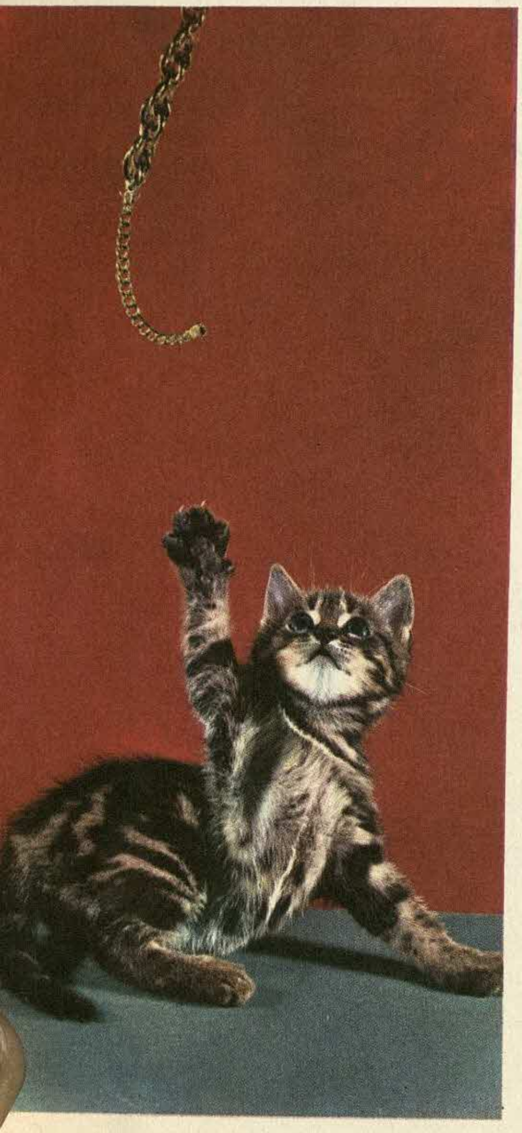
A primary biological drive such as hunger increases in strength with increasing duration of food deprivation. If we consider curiosity as a primary motive in monkeys, we would expect that the behaviour that presumably manifests curiosity would become more pronounced after depriving the animal of the opportunity to look at events taking place outside the test box. And, indeed, this is what appears to happen. Monkeys were placed in the test box, but they were prevented from opening the small door for varying periods of time ranging from zero to eight hours. After a specified interlude, during which the animals could only see the interior of the box, the door was unlocked. Then the monkeys, when opening the door, could observe the antics of a monkey colony. In this study, the door automatically closed six seconds after it was opened. Once closed, the monkeys could open it again at any time. The results indicated that the frequency of door-openings, a measure of the strength of the curiosity motive, increased as a function of the duration of visual restriction. Unlike the studies on food deprivation, the effects of depriving monkeys of a varied visual experience are most apparent within as little as two hours after the monkey was placed in the box. That is, response frequency to the door was much greater after the two-hour deprivation period than when there was no visual deprivation. The influence of visual restriction on behaviour probably would have been detected in even less time. Unfortunately, intervals shorter than the two-hour deprivation period were not in the experimental design.



Frequency of reactions as a function of the duration of the tests. Comparison between the curves of response according to whether the stimulus is food or visual. (From an unpublished study by R. A. Butler).



Apparatus used to determine the strength of the investigating drive in rats. S: starting-point, G: grid capable of administering an electric shock, M: maze to which access is the reward offered to the animal.



The playfulness of certain animals, such as this kitten, is obviously related to their natural curiosity. (Photo Lod).

Not only will monkeys work to see what is happening, but they will perform simple tasks for the benefit of hearing what is taking place. This phenomenon was demonstrated by placing monkeys in an enclosed box which itself was located in a sound-proof room. Inside the box were two levers. If the monkey pressed one of the levers, he was rewarded by twelve seconds of sound emanating from a monkey colony housed in an adjacent room. To provide this form of sound reward, a microphone was placed in front of the colony and a speaker was fixed to the box containing the monkey being tested. No sounds were produced when the animal pressed the other lever. The outcome of this experiment was that monkeys selected the lever which enabled them to hear the noise made by the monkey colony. When the auditory reward was made contingent upon pressing the previously 'silent' lever, they modified their lever-pressing behaviour.

To account for the results of these studies on sub-human primates, it does indeed seem necessary to postulate the operation of a curiosity motive. Furthermore, since responses to visual, auditory, and manipulative incentives can persist day after day, the curiosity motive seems to be a basic mechanism.

Curiosity in the rat

This research on sub-human primates is both exciting and refreshing. It deals with a form of behaviour that hitherto had received little or no careful investigation. More important, the experimental results strongly suggest that curiosity, which is so apparent in man, also operates in other primates. It would be a gross mistake, however, to assume that only the primates participate in exploratory behaviour for much research along this general line has been done with other animals. The rat, a most inquisitive animal, has been a frequent subject for these investigations.

One of the earliest studies suggesting the presence of curiosity in the rat was reported by Nissen in 1930. He built a maze containing several small compartments and scattered about the floor of the compartments was sawdust and several different kinds of objects. This is precisely the kind of environment that is highly suitable for eliciting exploratory behaviour in the rat. Nissen was curious to know whether the rats would cross an electrically-charged grid merely for the opportunity to investigate the interior of the maze. Previous studies had shown that rats would certainly subject themselves to electric shock for food, water, or sexual satisfaction, and Nissen's experiment on exploration gave similar results. In other words, the rewards intrinsic to investigative behaviour were sufficiently strong to motivate the animals to cross over the charged grid. It was unlikely that these animals were searching for food or water since they had been satiated before the test session began.

Over twenty years elapsed before this line of research was resumed. During the interim, several references were made to the exploratory impulses of rats, but this usually happened when someone's results of a maze-learning experiment in rats failed to agree with the particular learning theory in vogue at the time. As a matter of fact, renewed interest in the rat's exploratory behaviour came about largely through the animal psychologists' persistent concern over the maze-learning ability in rats. It had been observed repeatedly that if food is placed in each arm of a T-maze (a partially enclosed maze constructed in the form of a T) the rat, when set down in the stem of the T would turn into one arm of the T and eat the food but on the subsequent trial the animal would be more likely to turn into the opposite arm of the T for food. (This behavioural phenomenon, incidentally, is called spontaneous alternation.) Why should the animal alternate between the two arms of the T when it can get food in either arm? Montgomery approached this problem by placing rats in mazes of several different shapes and he simply watched them move about. No food was available in any of the mazes, nor had these animals ever received food during their maze-running experiences. Under these conditions, Montgomery observed an interesting and illuminating event: rats tended to go to that unit of the maze which they occupied least recently and he interpreted this to mean that rats systematically explore their environment. Later, he showed experimentally that the exploratory or curiosity drive in the rat is probably the basis for their spontaneous alternation in the T-maze.

The problem of the two mazes

Rats, like monkeys, will learn simple problems when they are rewarded for correct responses by the chance to engage in exploratory activities. Again, the T-maze has been used to demonstrate this phenomenon. In this particular case, one arm of the T-maze led to a blind alley and the opposite arm led to a more complex labyrinth in which the rats were allowed to explore. The rat when reaching the choice-point of the T could not see which arm led to the labyrinth because a swinging door, at the entrance to each arm, blocked its view. The colour of the doors however, signified which arm to enter in order to gain access to the more complex environment. One door was painted black and the other white and by entering the arm containing the white door, the rat could continue on into the labyrinth. The subjects soon learned to choose the door which led into the arm that provided a variety of exploratory opportunities. Sufficient experimental controls were employed so that any colour preference or position preference on the part of the rat could not account for the results.

Another example of rats learning a simple task for exploratory incentives is furnished by the work of Myers and Miller. Rats were placed in a box that was partitioned into two compartments; a lever was located near the partition and depressing the lever served to open a door. Within a short period of time, the rats learned to operate the lever, thereby gaining entrance into the other compartment. There was neither food nor water nor a sex partner in the adjacent room, so it seems most likely that the animals learned to press the lever merely to go to a different place.

In fact, the authors of this study suggested that a drive to eliminate boredom may have accounted for the observed performances.

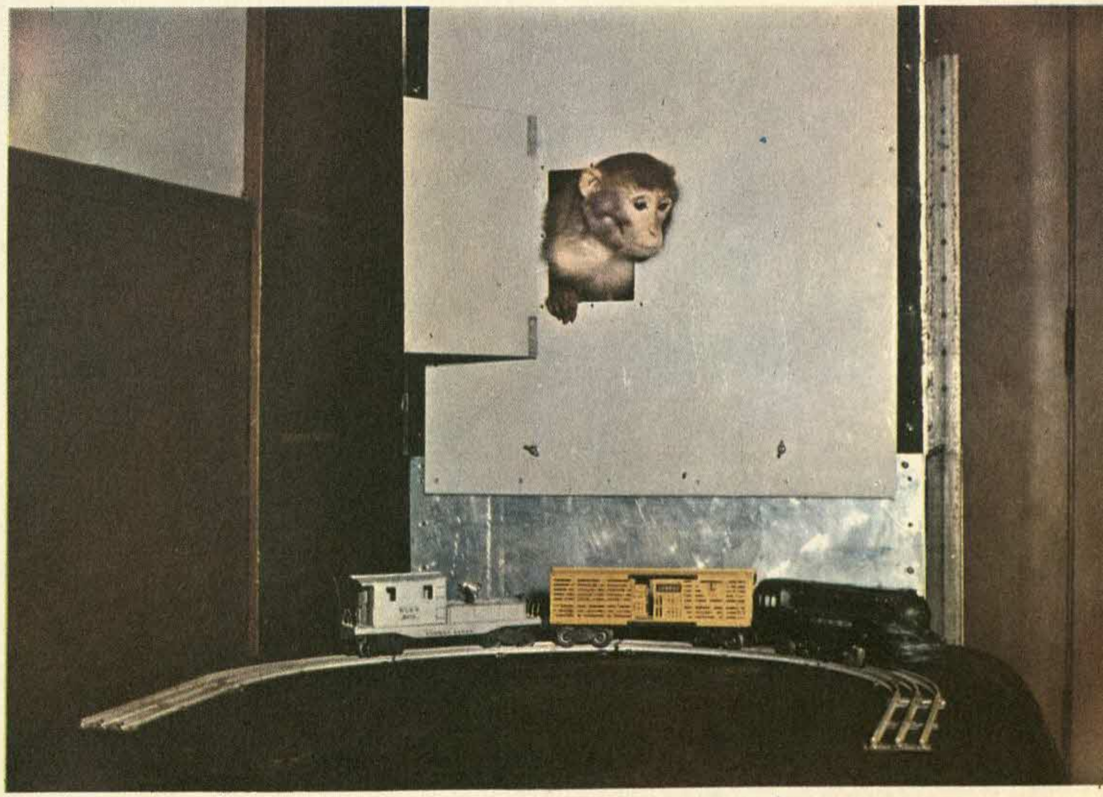
Several investigators have used a similar experimental technique to demonstrate that rats, as well as mice, will work to produce a change in the environment. The test situation is, indeed, a simple one. The animals are placed inside a darkened box which contains a lever and each time the subject depresses the lever, a small lamp in the box is illuminated for a brief interval. The results of this type of experiment clearly show that the frequency of lever-pressing is greatly increased when each response causes the lamp to go on. In this connection it is interesting to note that rhesus monkeys will operate a lever either to increase or decrease the illumination level. If pressing the lever fails to change the illumination level, the monkeys pay little or no attention to it.

As mentioned earlier, the manipulative behaviour of chimpanzees can be reinstated to its original level if the animals are permitted to play with new objects. The rat also is responsive to the presence of new or novel objects. Berlyne, for instance, exposed rats to familiar and unfamiliar objects and the amount of exploration, as measured by time spent sniffing each object, was recorded with the result that newly presented objects were explored significantly more than the familiar ones. In a more detailed study, the same experimenter measured the amount of exploration of an object as a function of exposure time. An object was placed in a small cubicle which was located in one of the walls of the animal's cage. The number of times that the rat approached the object was recorded automatically. The results of this series of observations demonstrated that the greatest amount of exploration occurs during the first minute and declines steadily thereafter. This evidence of rapid satiation to single objects further supports the general thesis of this presentation: that novelty is a crucial factor for eliciting exploratory behaviour.

Curiosity as a universal drive

Behaviour suggestive of exploration may exist in many, if not most, animals. The greatest proportion of research has been done on monkeys and rats. But these are common animals in psychological laboratories and, as a consequence, experimentalists have had ample opportunity to watch them closely. From everyday observations of kittens, one would expect that these animals too would be responsive to manipulative and exploratory incentives and data are now available which confirm this expectation. Kittens in a maze chose that route which contained objects that they take pleasure in handling. The objects, incidentally, were particularly attractive ones for kittens, consisting of a rubber ball, a

When it can observe some object to stimulate its curiosity—here a small electric train—the monkey manipulates the door most often. (Photo McGraw Hill Publications).



crumpled paper, a small box, and a piece of torn towel. A similar result has been reported for the racoon, an animal well-known for its fondness for handling things.

An interesting and provocative series of experiments has been carried out by Darchen with the cockroach. This investigator recorded the behaviour of cockroaches after placing them on a cylindrical stick, 92 cm long. The stick was floated on water in a tank and each observation period lasted for thirty minutes. His results showed that the amount of exploratory behaviour, as measured by the distance transversed by the animals, declined steadily as a function of time. Fatigue was not responsible for this decrease in activity, for when the cockroaches were placed on shorter sticks, they became less active much sooner. The activity level could be increased during the latter portion of a test session by any one of several experimental techniques. More specifically, if a differently coloured stick, a stick of different diameter, or a stick that differed in roughness, was substituted for part of the original stick, the declining trend in activity level was abruptly reversed. In general, these data parallel those collected on rats and primates in that responsiveness to stimuli decreases with familiarity, but it can be reinstated by the introduction of new stimuli.

Taken together, these experiments not only demonstrate that animals are alert to environmental change, but that they will work to produce a difference in their surroundings. It would be most misleading, however, to leave the reader with the impression that animals continuously approach and investigate all new stimuli; for even the most casual of observations would refute such a claim. Furthermore, in some instances, animals would be courting disaster should they approach strange objects indiscriminately. Several studies indicate that exploration can be suppressed by new and presumably fear-evoking situations. The rat, when placed in unfamiliar surroundings may, at first, remain motionless and if given the opportunity to occupy a sheltered cubicle, it will usually do so. Only later will the animal leave its sanctuary and start to explore. Moreover, behaviour interpreted by the experimenter as evidence for exploration may, under some conditions, be an attempt to escape from the test apparatus. Monkeys, too, are unquestionably reluctant to open a door to see fear-evoking stimuli and will press a lever less frequently to hear sounds indicative of potential danger than they will to hear meaningless noises. Infant chimpanzees fear novel objects but eventually will commence manipulating and playing with them.

Curiosity as a primary or secondary motive

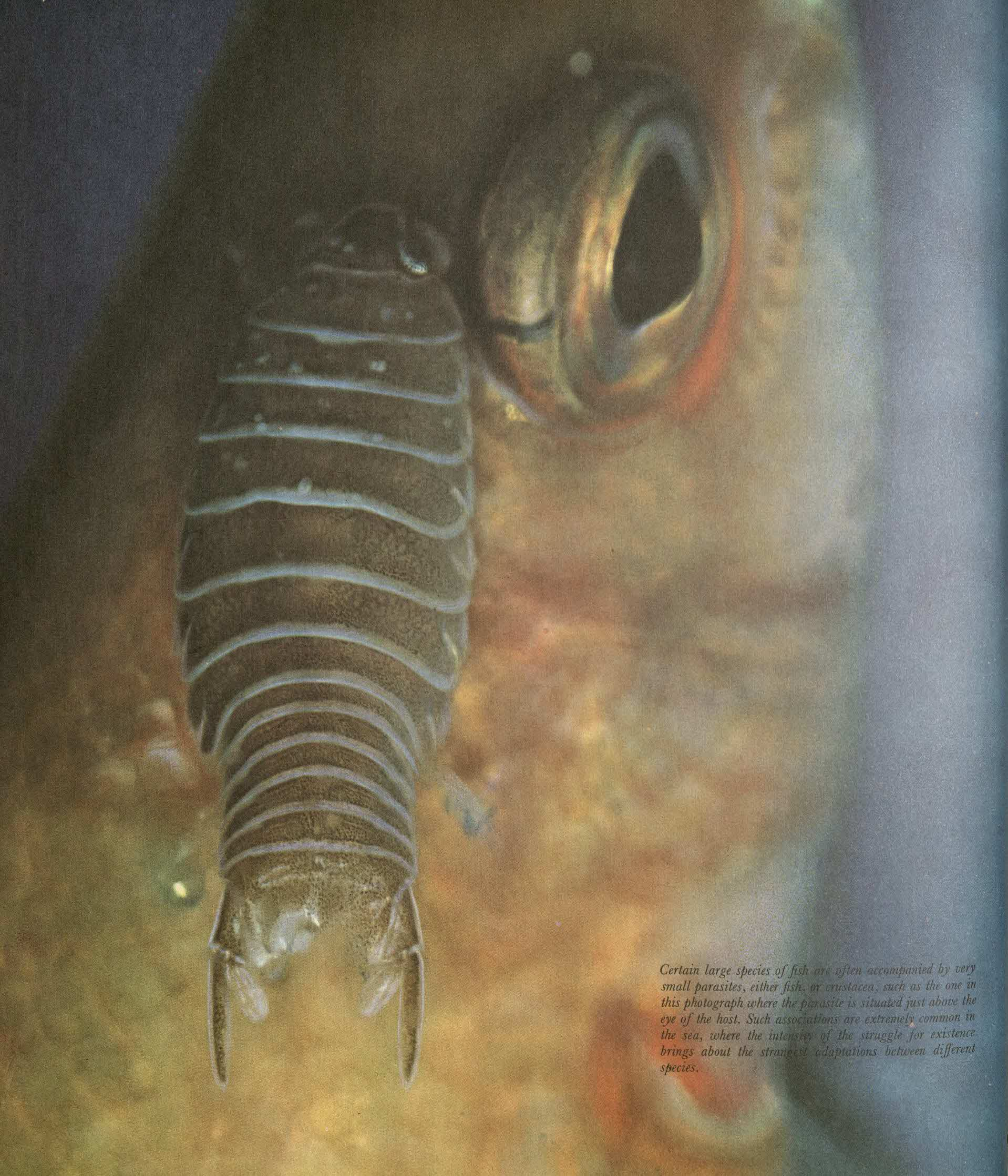
A number of psychologists maintain that exploration or curiosity is not a primary motive but that it is conditioned by the primary drives such as hunger, thirst, and sex. Exploration along with manipulative activity certainly can be of service to animals in securing food, water and sexual satisfaction, but this does not mean that the investigative activities represent nothing more than a set of learned responses that have, in the past, enabled the animal to satisfy its basic needs. Harlow and his co-workers have shown, for example, that infant monkeys, even before they have ever experienced solid food, will readily engage in manipulative behaviour. The question of whether hungry rats will explore more than satiated animals is still being disputed, with the differences in the experimental results being attributed to specific differences in experimental conditions. However, it is interesting to note in this connection that rats when hungry and thirsty will participate in a considerable amount of exploratory behaviour before they settle down to eat and drink. Generally speaking, the experimental data indicate that the presence of other motivations may either facilitate or inhibit exploratory behaviour but the manner in which these various motivational mechanisms interact remains indeterminate.

In conclusion, it should hardly come as a surprise to find that animals other than man exhibit curiosity. Rather, a motive as pervasive as curiosity, if emerging only at the human level, would be in direct opposition to the general and well-documented theme of biological continuity throughout the phylogenetic scale. What should be emphasised, however, is that curiosity, as illustrated by these experiments, does not signify an intellectual achievement. Animals are basically investigative creatures. Those that have highly developed perceptual and motor capacities are able to interact more thoroughly with an expansive and diversified environment; they can modify their surroundings in many different ways and can perceive relationships between specific acts and their consequences. Man is probably no more curious than many of the other animals. He simply has the biological means to acquire more information and utilise it effectively for gaining control over his environment.

PART THREE

Views of animal life

In the hive: bees on the cells of the honeycomb, magnified ten times. (Photo Lod).



Certain large species of fish are often accompanied by very small parasites, either fish, or crustacea, such as the one in this photograph where the parasite is situated just above the eye of the host. Such associations are extremely common in the sea, where the intensity of the struggle for existence brings about the strangest adaptations between different species.

Parasitism and symbiosis

Jean G. BAER

> *'Parasitism is the most spectacular demonstration of evolution. Its starting point is known from the free-living forms related to the parasites'.*
>
> MAURICE CAULLERY

Flea, louse, bug, tapeworm, tick, leech, even the names of parasites repel us, for the popular idea of parasites is of unpleasant creatures which suck blood or thrive in the intestines, creatures so degenerate that they cannot live independently and must find their food and shelter at the expense of another, somewhat cynically described as their host. Indeed, at one time the existence of parasites seemed so mysterious and their structure so unlike that of free-living animals, that it was thought that they must be sports of nature arising purely by chance and not subject to the ordinary laws of biology.

Nevertheless, for biologists parasites provide one of the most fascinating of studies because the variations in the intimate relationships between parasites and their hosts is truly astonishing. These relationships are necessarily carefully balanced ones; for if the parasite is too destructive whilst living at the expense of its host, it will destroy that which is essential to its life and prejudice its own survival. Accordingly, parasites have evolved in conjunction with their hosts and it is possible to study the way in which they have adapted themselves compared with their free-living relatives.

There is no basic structural plan common to all parasites since they have arisen from most classes of invertebrates. Yet, in spite of their different origins, there is a tendency for them to have certain characteristics in common. For instance, organs which are no longer required for parasitic life, such as legs, eyes, and wings, tend to be lost or reduced.

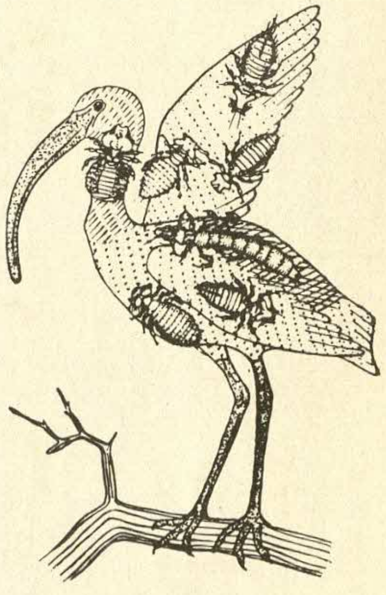
Associated with this degeneration of sensory and locomotory organs, other organs develop new functions or increased capacity. This is particularly true with respect to reproduction, nutrition, and the development of organs of attachment. Nutritional adaptations are common because parasites depend on their hosts for their essential nutrients, and must be suitably equipped to obtain and utilise them. They may be physiologically adapted so as to be able to exist on one particular type of food and structurally modified in order to obtain this from the appropriate part of their host, to which they may fix themselves by specially modified organs. For example, some parasites can live on blood, and may be found either inside the blood vessels or on the skin, but in the latter case they must have an organ to suck blood. One of the major difficulties confronting parasites is ensuring that they can be transmitted to another host. This is usually a hazardous process and in consequence parasites commonly have greatly increased reproductive powers.

Relationships between host and parasite

This chapter is devoted chiefly to the synchronisation between the life-cycles of parasites and their hosts; for these interrelationships show the nature and extent of adaptation to the parasitic way of life more clearly than merely listing the various structural peculiarities. These life-cycles are often very complicated, as the parasite larvae usually need different food from that required by the adult form. To overcome this, the larvae may be sheltered by a different species of host from the adults, so that the life-cycle includes an alternation of generations.

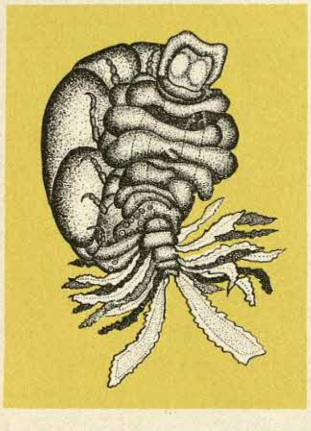
The type of life-cycle differs according to whether the adult is an *ectoparasite*, living on the surface of its host, or an *endoparasite*, living in the tissues or body cavities, but the same biological laws relating to their survival apply.

Among the ectoparasites, there is one group of lice which feeds on blood and another which lives on feathers or hair. In the latter case, the eggs are attached to the feathers or hair and survival is ensured because when the young louse hatches it can find food without leaving its host and proceed to infest it straight away. The female human louse lays about 300 eggs, each of which gives rise to a mature adult capable of reproducing itself within about eighteen days, but the density of the louse population is limited both by the amount of nourishment available and their destruction as a result of host activities, such as scratching.



An old drawing showing the distribution, on an ibis, of different louse populations, according to the region of the body.

A classical example of symbiosis: the hermit crab, which finds a home in the empty shells of other crustaceans and 'uses' the Actinia *(sea anemone) to protect it against many predatory species. (Photo Lod).*



Cepon elegans: *an egg-bearing female and dwarf male.*

Isolated on their host in this way, lice have specialised into morphological types adapted to their particular localisation or habitat. For example, on birds, some lice populations are adapted to the head and neck feathers and others to the wing or body feathers. It is only by contact with a host which already has lice that a new host can become infested. However, the survival of louse populations on their particular host species is ensured by being passed from parents to offspring.

The life-cycle of ectoparasites

When the eggs of ectoparasites are not attached to their host, the life cycle is complicated because part of it takes place away from the host in the surrounding environment. When the host is a land animal, as in the case of the bird fleas and the mammalian fleas, the eggs fall into the nest or lair where the larvae hatch and feed on scraps and particularly on moulds, which provide vitamins essential for their development. Adult fleas feed exclusively on blood and find their hosts in this way without difficulty. They also have a phenomenal capacity for fasting. For instance, the fleas of migratory birds will remain alive in the deserted nests until the birds return in spring.

As a result of this type of life-cycle, flea populations are to some extent isolated from each other and this leads to the formation of many different species. However, such isolation may equally well arise because a flea will not take in blood unless it is of the exact composition peculiar to its most favoured host. The reason for this has been very little studied.

Aquatic ectoparasites face different problems. For example, the Monogenea are very small flat worms, which live attached to either the gills or body surface of a fish, where they feed on blood or mucus. They lay their eggs directly into the water and, since the eggs may have long filaments on them, they soon become entangled and form masses on the bottom. The larvae are covered with vibratile cilia, so that they are able to swim in search of a favourable host and when they find one, they attach themselves to it, lose their cilia and develop into adult parasites. Contrary to what one might expect, the Monogenea have quite specific hosts. This seems to be because the favoured host has blood or mucus of some special chemical composition, as well as structural peculiarities in the shape of the gills.

Some Monogenea have become secondarily adapted to live on frogs, but, as the latter only live in water during the reproductive period, the parasite's life-cycle has had to be adapted to these new conditions. For example, one worm known as *Polystoma*, takes refuge in the frog's urinary bladder. It lays its eggs as soon as the frog enters the water, so that they then fall to the bottom of the pond. The ciliated larvae hatch at the same time as the tadpoles and attach themselves to their gills. The tadpoles grow slowly larger and, when the gills disappear as they change into frogs, the larvae enter the mouth, pass along the length of the intestine and penetrate into the bladder to complete the cycle.

Tadpoles are always more numerous than *Polystoma* larvae, but the worm has a way of greatly increasing its chances of survival, for if its larvae attach themselves to the gills of very young tadpoles, the reproductive glands of the larvae mature precociously and they lay eggs whilst retaining their larval form. This precocious maturation is known as neoteny, and enables *Polystoma* to parasitise more tadpoles before they metamorphose into frogs.

The increased number of eggs produced by ectoparasites is also found among the Isopoda, or sea-lice, crustaceans which are parasitic on other crustaceans. During the incubation of the eggs the female holds them against her abdomen by means of leaf-shaped appendages, but the number of eggs is so enormous that these appendages grow disproportionately and the female body becomes deformed in a way which never happens in free-living Isopods. Indeed, the mass of eggs is so huge that it dwarfs all other structures.

A survey of the life-cycles of ectoparasites shows that if the eggs are not attached to the host the ectoparasites can only survive by increasing their reproductive powers. This is most noticeable when the eggs hatch at some distance from the host, and the chances of the larvae meeting a favourable host are greatly reduced, as occurs in certain aquatic parasites.

Endoparasites

Endoparasites do not fall into the same groups as the ectoparasites, but their life-cycles obey the same laws, although they are often very complicated and require many different ways of reaching their hosts.

The maggots of certain flies, the gadflies, are parasites in the nasal cavities or stomachs of ruminants, such as sheep, deer, and horses. These flies lay their eggs near the mouth or nostrils, so that when the animal licks its lips it takes in the larvae, which then attach themselves to the lining of the nasal sinuses or stomach, where they continue their development. When the maggots begin to turn into flies, they detach themselves, and are expelled by sneezing or pass out of the body with the dung, and complete their larval existence in the soil.

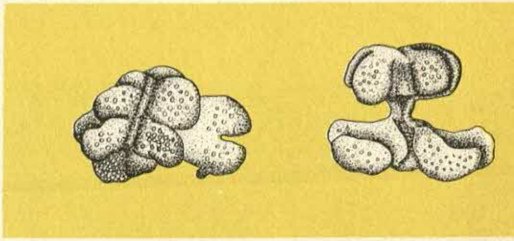
One particular species of gadfly lays its eggs in the thigh region of cows and the young larvae burrow through the skin and move along the nerve of the leg until they reach the skin of the back. While it is growing the maggot needs air, so it perforates the host's skin. This forms an abscess, which bursts. Expelled, the larvae complete their development in the soil.

Numerous round worms live in the intestines and lay eggs which hatch in the faeces, so that the larvae subsequently develop in the soil. Eventually, they rise to the surface and penetrate the skin of mammals lying on the ground or the soles of men's feet. Being very small, the larvae are carried by the circulation to the lungs where they cross the boundary between blood and air and pass into the bronchi or breathing-tubes. By this route they reach the mouth, when they are swallowed and reach the intestine, where they grow into adult worms. This is how infestation is maintained among the members of a primitive community and their animals. But, although man and dog harbour distinct though very similar species, the complete development of larvae in an abnormal host is prevented by a physiological barrier, represented by a skin reaction.

However, the larvae of the vast majority of intestinal worms can only continue their development outside the intestine in the body of a second host, termed the secondary, or intermediate, host, which, by consuming eggs or larvae, permits their development up to the next stage. The cycle continues, when the intermediate host is eaten by a new host belonging to the same species as the animal which harboured the adult worm and is called the primary host. When the adult worms mature in the tissues rather than the intestines, as in *Filaria*, they produce larvae instead of eggs, which pass into the blood-stream. In this case the intermediate host is a stinging insect, which takes up the larvae while feeding and passes them on when it feeds again.

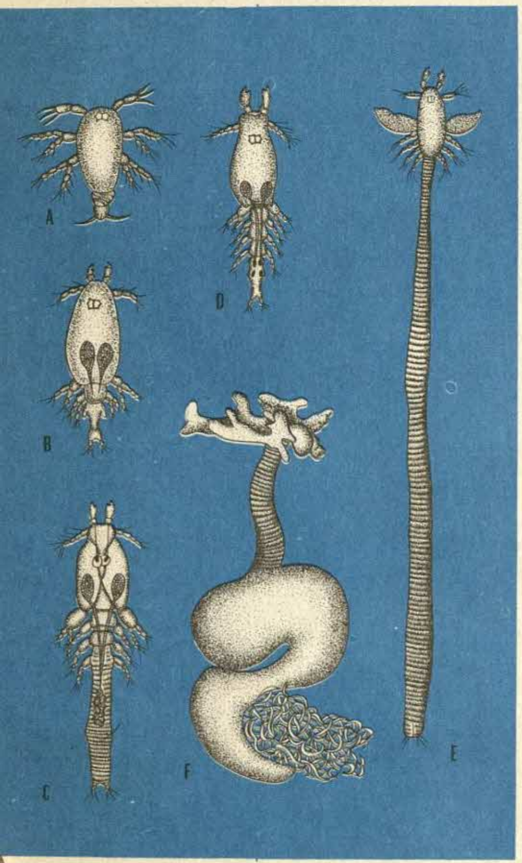
Sometimes there are two successive larval stages, each in a different intermediate host. This occurs among solitary worms with aquatic life-cycles. The first host is an invertebrate and is eaten by the second, which is a fish. One well-known species, *Bothriocephalus*, the Russian tape worm, lives in man, who is infested by eating raw or semi-cooked fish. This type of cycle differs from those previously described in that there are three successive hosts instead of two.

If a life-cycle, which takes place partly in intermediate hosts, is to have some chance of



Ancyroniscus bonnieri: *egg-bearing female.*

Lice are common parasites, adapted to many different species. Here are two Dolpocephalia of the hen, enlarged about twenty times.



Lernaea branchialis.
A, nauplius (larva). B, young female. C, fertile female leaving its first host. D, male coming to maturity. E, fertilised female attached to secondary host. F, mature female. (From Scott).

completion, it is obviously essential that these hosts are included in the food chain of the primary host. Even under these conditions, the risks of breaking the cycle are enormous, in spite of the increasing fecundity of the intestinal worms, which lay eggs continuously. A *Botkriocephalus* may produce tens of thousands of eggs every day, but the proportion of larvae which eventually arrive in the intestine of a favourable host is less than one in a million. In comparison, several species of small-sized solitary worms produce relatively few eggs and there would be a very remote chance of their life-cycles being completed, were it not for the ability of the larvae to reproduce by budding. As a result, massive infestation of the definitive host follows after only one intermediate host has been eaten.

The most complicated life-cycles include two intermediate hosts and successive larval forms, together with one free-living phase. This occurs among the flukes, or Trematodes, which are flat non-segmented worms living in the body cavities of numerous hosts, including man. The first intermediate host is always a mollusc and the larvae which hatch from the eggs of the parasite have the remarkable power of being able to multiply while continuing their development, until they grow to the stage where they look like minute flukes with tails, known as cercariae, which can penetrate into the second intermediate host. Consequently, in a suitable mollusc, a single larva may produce some thousands of cercariae which escape into the surrounding environment. However, only a small number of these cercariae reach the second host, which must be eaten in its turn by the primary host before the cycle can continue.

There are several variations in this type of cycle, but these usually relate to the stage after the liberation of the cercariae from the mollusc. Rarely the second host may be omitted, and the cercariae penetrate directly into the primary host, where the worms grow into adults in the blood vessels. Sometimes, there is a third intermediate host, making the cycle even more complicated and resulting in an enormous wastage of larval forms.

In all parasite life-cycles there is a correlation between the degree of fertility of the parasite or the capacity of its larval forms to reproduce, and the degree of destruction of larvae before reaching their favourable hosts, either intermediate or primary. This correlation demonstrates how parasites have become adapted to their particular mode of life, and the same selective mechanism operates that is responsible for the distribution of the rest of the animal world. How often the cycle is completed depends on the extent to which the primary host is integrated into the surroundings where it lives with the intermediate hosts. It is because of the similar ecological associations of the hosts that parasitism has been able to spread and parasites to infest new hosts.

However, as the physiological needs of parasites become specialised, the number of favourable hosts is restricted and, consequently, selection intervenes in the choice of successive hosts. This results in a varying degree of isolation of the parasite in either one, or in a group of particular species. This confinement to specific hosts has favoured the evolution of parasites into very numerous species. Genetic isolation, comparable to that which occurs in island populations, has led to the appearance of parasitic fauna endemic to specific groups of vertebrates.

Parasitism has appeared many times in different classes of animals and results from the loss of the ability to synthesize certain indispensable elements for themselves. But, although parasites are incapable of an independent existence and are highly specialised animals, their survival is subject to the same biological laws as those which control free-living organisms.

Symbiosis

One particular form of co-existence is the reciprocal association of two organisms, known as symbiosis. In this situation both partners are adapted to each other and each benefits by obtaining from the other elements which it cannot synthesise itself.

It is only because the primitive insects and ruminant herbivorous mammals have formed symbiotic relationships with bacteria and protozoa, that they have been able to survive on a diet composed mainly of cellulose, which constitutes the woody supporting tissues of plants and grass. Their own digestive tracts cannot utilise cellulose until it has been broken down by these organisms, and this is why numerous bacteria and protozoa are found in certain regions of their intestines. Attempts have been made to separate the partners in such associations experimentally and to maintain each of them independently, but they have usually failed.

The biological importance of symbiosis is that it enables various important groups of insects and mammals to adapt themselves to a specialised diet and to occupy niches where there is little pressure from the competition of other animals.

The migration of animals

Jacques LECOMTE

The term migration covers a number of very diverse phenomena. To begin with, it is necessary to distinguish between once-only migrations and those which involve going and returning. In this chapter, the word migration will be used in the latter sense and the term exodus will be reserved for the once-only migration. However, before discussing the complex problems which face zoologists in the coming and going of vast animal populations, it is worth mentioning some examples of exodus.

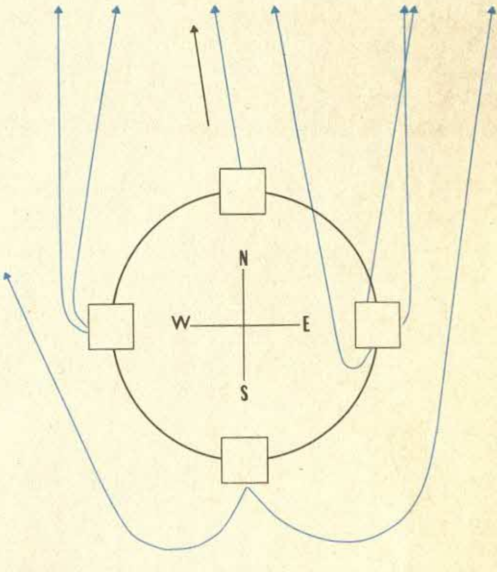
But here, too, a further distinction must be made. One type of exodus takes the form of the expansion of a species which, more or less rapidly, invades wide areas of territory for reasons that are largely unknown; the other is the even stranger case of hordes or swarms of animals, such as locusts, butterflies or rats, engaging in a mass movement, for equally incomprehensible reasons, and disappearing rapidly into the desert, the sea, or simply into the jaws of their predators. As an example of the first type of exodus we may take the armadillo, which, being slow-moving, peaceable, and reproducing itself relatively slowly, one might expect to be an animal which is likely to become extinct. Yet precisely the opposite is the case: towards the end of last century it left its original Mexican habitat and invaded Texas, in 1926 it was in Louisiana, and in 1936 it crossed the Mississippi. By 1939, it was in Florida, and it only stopped around the 33rd parallel because of the severe winters.

The disappearance of an indigenous species following the immigration of another is a common phenomenon in nature. Thus the introduction of the sparrow and the starling from Europe into North America was carried out at the expense of the local fauna and similarly, the introduction of a European butterfly, the cabbage butterfly, into the United States has led to a considerable reduction in the number of related indigenous species. Another curious example is that of the war between the black and brown rat. The black rat, which dominated Europe in the Middle Ages, carrying the fleas which spread the Black Death, has almost completely given way to the brown sewer rat. This latter species was reported in Paris for the first time in 1793, but it has increased with a surprising rapidity and today the black rat is a relative rarity.

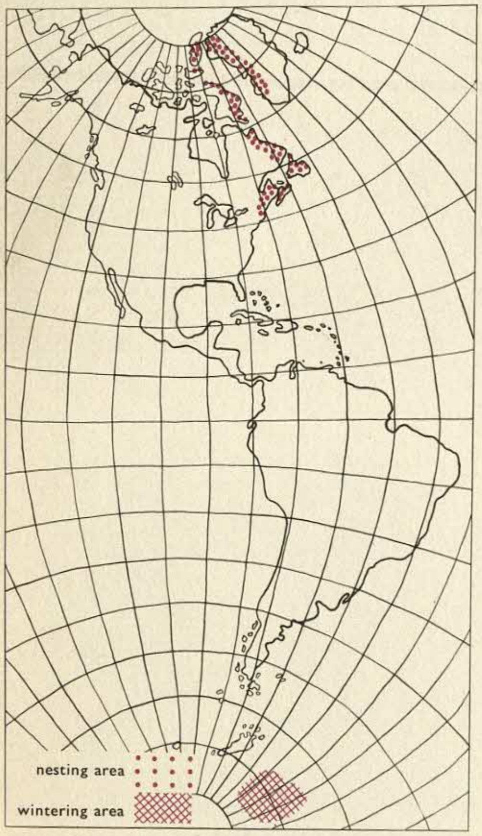
What are the causes of these remarkable invasions and retreats? It would be incorrect to say that we know all about this subject, but a fair number of hypotheses can be put forward. Thus, the armadillo apparently profited from the biological disequilibrium[1] created by North American civilisation: the extension of land cultivation and the consequent destruction of the carnivores which were its natural enemies, are in all probability the reasons for its success. In the same way the doryphore,[2] a small harmless-looking beetle, is another of the beneficiaries of civilisation.

So far as the rats are concerned, the story is a complex one, which seems to illustrate the hierarchy of species: the general law that, if two closely related species live together in the same region, one will sooner or later drive out the other. It must be added, however, that cats show a marked preference for the black rat, and this aspect of feline gastronomics cannot be overlooked. Furthermore, the war of rats is not yet over; for the black rat now lives in barns, having abandoned the sewers and gutters to its brown rival, and recent reports from Germany and Switzerland point to a definite trend towards a renewal of its supremacy.

The exodus of the second type does not result in the extension of the species, and the result of these invasions is generally catastrophic: the classic example is that of the migratory crickets. The appalling ravages by locusts are understandable when one considers their number, since a cloud of locusts is, in effect, a universe in movement, and the weight of one of a single swarm has been estimated at about 35,000 tons. What is the origin of these clouds of devastating insects? The biologist Uvarov in 1921 showed that solitary locusts and the members of these vast armies are not two different species but two aspects or phases of the same creature, and Rémy Chauvin, in 1941, demonstrated the mechanism and magnitude of this transformation. Not only has the gregarious animal a different colouration from the solitary form, but its physiology is completely different; it eats more, develops more rapidly, and lives for a shorter time than the solitary form.



Direction of flight taken from the time of departure by homing pigeons more than 300 km from their base. The small arrow indicates the direction of their loft. (After Kramer).



The longest bird migration known is that of the sea swallow, Sterna paradisaea*, which travels virtually from the North Pole to the regions of the South Pole and back, no less than 12,000 miles. (After Cooke).*

The influence of microclimates

How does the transformation occur? Apparently the cause is the sensory excitations provoked by the sight of, and contact with, other animals of the same species. Thus a cricket reared in a glass tube in the middle of a cage full of other crickets becomes gregarious when exposed to light, but in darkness it remains the solitary type of animal. On the other hand, if it is in direct physical contact with other living crickets, it becomes gregarious even in darkness.

Again, in certain zones, due to a particularly favourable microclimate,[3] types of larvae are produced which associate together before flight and, having acquired wings, spread desolation over a wide area, subsequently disappearing without trace.

Another example, less well-known and less well studied, if equally curious, is that of the lemming. This little rodent lives on the plateaus of the Scandinavian peninsula where normally, it leads a peaceful and timid existence. It comes out only at night, or at least during the darkest hours of the northern days, and many naturalists have crossed Scandinavia from one side to the other without even suspecting its existence. Suddenly, every three, four or five years, and without knowing why or where it starts, one finds lemmings everywhere: they come out into the sunlight, are apparent to every one, and leave their mountainous plateau to descend into the valleys and regions rich with crops. If famine were the reason for their movement, if a sudden and inexplicable increase in their birth rate were the reason for their exodus, one might expect them to stop there, but this is not the case and a compact horde continues as far as the sea where the tale almost invariably ends in mass drowning.

Other examples abound: the exodus of squirrels, armies of field mice or of birds such as Pallas's sand-grouse and the crossbill. A particularly interesting example is a butterfly of the genus *Danais*, that forms in some way an intermediate link between the two types of migrations, the exodus and the going and returning (a fact which demonstrates once more that the phenomena of life are extremely difficult to classify into well-defined categories). The going and returning, in the case of these American butterflies, is not carried out by the same individuals but by two generations. Those butterflies which leave their place of birth to go to the south of the United States, reproduce and die. The following generation returns.

This migration is also marked by a very curious fact, the existence of special 'butterfly trees' which are used by successive generations along the route of their migration as places of assembly and rest. Without surrounding them with superstitious veneration as the local Indians did, we may well ask ourselves the reason for this choice and how they effectively carry out some sort of 'billeting-order'. So far as man is concerned, nothing distinguishes the 'special' trees from the surrounding ones.

This transition leads us to the discussion of large migrations where, the facts are many and the hypotheses so strange that it is difficult to cover them all.

The going and coming migrations

When we come down to hard figures, the record for migrations certainly goes to a bird, a swift of the Atlantic Ocean, which nests in the extreme north of Canada and winters in the extreme south, on the borders of the Antarctic continent. The distances covered by this bird's journey, carried out twice-yearly, is of the order of 12,000 miles and the accuracy of its navigation is remarkable; for we know that some swifts return to their nest every year. But even if the bird does not go by habitual routes, it does not appear to be unduly troubled, and in this respect, homing pigeons are perhaps less remarkable than the case of a puffin, which, transported in a cage from the island where it was born off the coast of Wales, to Boston in the United States, was found twelve days later in its hole—it had, in fact, taken only ten hours longer than the letter announcing its departure.

The most popular migrants in Europe are undoubtedly the swifts, the storks and the ducks. Living close to man, these birds have for a long time captured his imagination by their periodic disappearance and reappearances and given rise to some rather foolish folklore on the subject. Thus in the sixteenth century, the Swedish Archbishop Olaus Magnus announced that the swallow passed the winter in the depths of the sea, and even the great Linnaeus in the middle of the eighteenth century was prepared to support his compatriot. As late as 1817, the French naturalist Cuvier believed in this superstition.

Meanwhile, the supporters of the migratory theory (who had existed since classical antiquity) became more and more numerous. Buffon was one of the first scientists to concern himself with this field, and today migration is studied experimentally in many laboratories.

How migrations are investigated

There are three possible approaches to the study of migration: the descriptive study of the facts themselves, the study of causes, and the study of the processes involved.

1. *The facts*

This first approach is based essentially on ringing, and it is thanks to the incessant labours of those who ring birds and the collaboration of those who happen to recover them that we have been able to trace some of the migration routes.

The first person to carry out the scientific ringing of birds was the Dane Mortensen, who, in about 1890, marked a large number of starlings by means of a numbered ring. Today, however, a large number of stations concerned with ringing exist throughout the world. There are also a certain number of stations equipped with many different kinds of snare for recapture, but most often the ringed birds are found accidentally by hunters and the percentage of recovery varies according to the species. Thus it is 22% for cormorants and 16% for wild ducks but only 0.2 to 1.1% for the small passerines such as warblers.

In France, the research group working on migrations at the Muséum in Paris under the direction of Professor Etchecopar have ringed, between 1930 and 1955, about 155,000 animals, of which about 1% have been recaptured. Methods of marking have improved considerably and are now applied to very different species and embrace all groups from mammals and birds to fish and insects. Together with ringing, other methods, such as colouring, marking the ear or tail, and radioactive isotopes which permit one to follow or locate the animal by means of the radiations emitted are employed. Recently, a small capsule has been invented which emits radio waves and can be placed in the body cavity of certain mammals.

To these methods we must add the direct observation of the movement of birds. The flight of birds can be followed for quite long distances through field-glasses, successful observations can be made from an aeroplane, and more highly specialised investigation makes use of radar. In the early days, observers watching radar screens were often surprised to note 'phantoms' appearing on the screen which seemed to have no connection with any known object. These images, we now know, are produced in many cases by birds in flight, and their study has shown the frequency of nocturnal movements which, naturally enough, escape direct observation. In these ways we can make more and more precise maps of migration for a larger number of species ranging from the bat to the salmon, and, of course, the swallow.

The migrations of large mammals, particularly in the polar regions where they sometimes travel thousands of miles, have an impressive grandeur. Here is a herd of reindeer, crossing an arm of the Lapland sea (from Science et Vie*).*

2. *The causes*

It seems almost impossible to find any reason or logic behind migrations. Conceivably they may be due to the drift of continents or to glacial periods, but nothing could be less certain, and the only question to which it is possible to reply accurately concerns the physiological factors influencing the migratory impulse. Here the role played by the endocrine glands[4] is undeniable.

In birds, the pituitary gland at the base of the brain seems to have an important influence on migration, and Rowan in 1926 and Wolfson in 1941, to cite only two, have shown the remarkable role of the endocrine glands in migratory birds. The same is true of fish, as for example was shown by the work of Fontaine, who has clearly demonstrated the part played by the thyroid gland in initiating the migration of the eel and the salmon.

3. *The processes*

There remains the problem of 'how': how, in fact, is it possible for a salmon to return

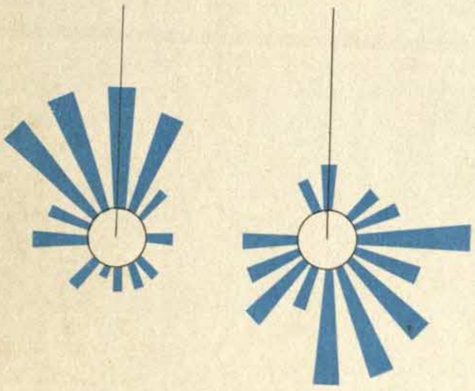
(1) Biological disequilibrium. *In a given territory, there exists a relationship of forces between carnivores, herbivores and plants. The biological equilibrium is upset when the proportions are altered in one way or another.*

(2) Doryphore. *See the chapter entitled 'The Biological Struggle'.*

(3) Microclimate. *The climate of a restricted region as compared with the general climate of the geographic region.*

(4) Endocrine glands. *Glands of internal secretion. They secrete into the blood the important substances known as hormones.*

unerringly to the exact tributary of the river where it was hatched, after long spells in the ocean? How does the swallow find its own nest in the eaves of your roof after several months spent thousands of miles away? We can only consider here the case of birds, about which most information is available. Apart from the true migratory species, we can study birds like the homing pigeon, which return to their base by what is presumably the same sort of mechanism. The advantage of carrying out experiments with domestic animals which can be raised in large numbers is obvious, and there is no lack of explanatory theories. One of the earliest assumed that birds are capable of detecting the magnetic pole or can follow a hypothetical 'electro-magnetic current', but these hypotheses have been proved untenable by a very simple experiment, which consisted of attaching a magnet to the foot or the neck of the pigeon in order to upset its supposed ability to detect natural magnetic fields. Despite this, the return to the nest was carried out perfectly normally.



The effect of cloud on the orientation of puffins. On the left—clear sky. Most of the birds from the moment of release take the correct direction (vertical line). On the right—very cloudy. Most of the birds are disorientated and take a false direction. The length of the dark sections is proportionate to the number of birds taking flight in a specific direction. (Matthews, 1953).

A second hypothesis is based on the existence of the Coriolis force, produced by the rotation of the earth. It seems impossible to believe that birds have the ability to discern the slight variations in this force, but drifts observed in migrations have been explained by the fact that the air masses tend to be carried from north-east to south-west. Unfortunately for the holders of this theory, the Coriolis force could only influence the body in full flight and it is well known that the tendency to proceed from the north-east to the south-west exists even in wingless birds which are incapable of flight. Clearly it would be tedious to enumerate all the many possible hypotheses and we must now go on to discuss the more modern views.

The problems of navigation

As noted by G. V. T. Matthews, a specialist in this field, human navigation has for centuries been based on the method of determining position in relation to the sun. But, it has only recently been suggested that birds, too, may navigate by this method. If this were the case the essential element for orientation would be the solar arc, that is to say the apparent trajectory of the sun.

This arc lies at a certain angle in relation to the horizon and it is the measurement of this angle, constant for any given place, which enables us to calculate the latitude of that place, and from north to south the angle becomes greater. Thus if a pigeon is able to recognise the arc in the region of its loft, it will be able to go north or south according to the arc which it finds in an unfamiliar area. Similarly, from the observation of the trajectory of the sun or a part of its trajectory, and by precise knowledge of the solar arc at a particular point, it is possible for the bird to judge its position relative to east or west. Since the height of the sun depends upon the time of day, we must also assume that the bird possesses some sort of 'internal chronometer'. This is quite feasible because several animals are known to possess such an apparatus, as for example the bees.

It has also been proved that the visual acuity of birds is sufficient to measure very small angles and that their perception of movement is much better than that of man. Furthermore, high-speed film has shown that the head of a bird always remains perfectly horizontal during flight, even when the body is not, and it is known that a very delicate mechanism of adjustment permits the muscles to maintain this position with the help of information supplied by the inner ear which is the main organ of balance. Thus there is created a sort of artificial horizon, comparable to that used by air pilots who have no horizon, or sailors who rely upon the surface of the sea. This theory is perfectly plausible, but one has to have been a captain on long-distance sea-voyages to grasp all the intricacies, and then be prepared to admit that birds throughout the ages have known more about the subject of navigation than 99% of humanity!

Of course, in scientific research, there are always some objections which can be brought against a theory, and in this case the most obvious one is: how do the birds manage when the sky is cloudy? The fact, however, is that under these conditions they seem very disorientated and it is common knowledge that the return of homing pigeons is delayed, so the argument actually supports our theory. Another criticism is more difficult to answer, namely the case of nocturnal migrations, which radar observations have demonstrated to be quite common. Here we are forced to accept the improbable, but only rational hypothesis, that the birds orientate themselves in relation to the stars.

This brief account brings us to a realisation of the magnitude of the problems presented by animal migrations. Biology, physiology, animal psychology, astronomy: it is clear that many sciences must be brought in to penetrate the secret of these strange and still mysterious movements.

The social insects

Rémy CHAUVIN

The attention of man has always been fascinated by social insects and particularly by bees and ants. Who has not stopped before a busy ant hill, to get up after a time surprised, troubled, and vaguely distressed? Bees may appear more reassuring because man has been familiar with them for so long, and also, doubtless, because of their honey. But bees, ants, termites and wasps all present the spectacle of that organisation and inexorable industriousness which are something terrifying. We are fortunate to be protected by the smallness of their size; what would our woods and fields be like if red ants were the size of mice?

The distinguishing feature of social insects is that they live together in large communities, sharing the tasks of construction, food gathering and other activities.

We shall give some examples of this co-operation and some striking figures of the growth of population and accumulation of food among social insects, before going on to treat of their psychology which is only a group psychology, for nothing is more stupid than the bee or ant isolated from its community.

A mass phenomenon

Five thousand bees weigh a pound,[1] and a good hive at the height of the season contains 10 to 15 lb, that is to say, 50,000 to 70,000 bees. This is equivalent to an animal the size of a dog, but with a far higher rate of metabolism, in each hive. The colony sends out emissaries to collect nectar and pollen—20 to 30,000 (4 to 6 lb) per hive. Each makes two to five trips a day and brings back a relatively tiny load each time, but their combined load represents an astronomical figure in proportion to their body-weight. In fact, each hive needs about 450 lb of nectar and 90 lb of pollen a year, that is, about forty times the weight of the colony, the total harvest being gathered almost molecule by molecule from the nectar glands of flowers, or grain by grain from the anthers which produce pollen. These provisions, which appear relatively enormous, are necessitated by the very rapid rate of development of the hive. In fact, the queen lays 1,500 to 2,000 eggs a day, and several bees hatch out each minute throughout the day and night, so that during the whole of the season it is necessary to provide energy-containing food (sugars from nectar), and food necessary for growth (the proteins of pollen).

However, the bee has been parasitised for several thousand years by another social animal, man, who has as strong a taste for honey as the bee itself. It has been calculated from reliable but incomplete statistics that in France alone 25,000 tons a year, and perhaps two or three times more than that amount, is removed from the hives.

Recently, a food product has been made

Bees, magnified three times, busy with the maintenance of the comb. (Photo Lod).

from pollen collected by bees. A simple hives some of the pollen collected, and in this way 4 oz or more can be harvested daily from each hive during the peak season. In France alone, 20 to 30 tons a year has easily been collected in this way and, if pollen were harvested from all the hives the figure would be 50 to 100 times greater.

The statistics of ant communities are less well known than those of bees. In the case of wood ants, which roof their homes with twigs, the worker ants carry pieces of insects to the nest to be eaten there. German research workers have calculated the quantity of 'insect meat' thus transported to be about 25 to 32 oz a day per nest, the population of the nest being 300,000 or even 600,000 ants. Others have found that these insects, which choose their food carefully, also store honeydew,[2] a sugary secretion of certain aphids or plant lice and one nest consumes at least 200 to 400 lb of it in a year.

If little is known about ants, even less is known about termites, save that they are almost alarmingly abundant in nature.[3]

Socialised work: construction

One of the most striking activities of social insects is nest-building, some of these nests, particularly those of termites, being of considerable size. Thus the nest of a certain *Polybies* (American wasp) is an immense sort of box-like container about the size of a man and suspended from a branch by a robust 'handle'. Many of these nests are extremely complex and some are so regular in design that they seem man-made.

Termite nests, too, have a distinctive architecture and consist of a central region filled with cavities of various sizes, rather like a sponge. This is surrounded by an external layer which, in some species, is riddled with an amazingly regular system of galleries and columns. In the big nests of *Bellicositermes*, one oval space, the royal chamber, is found in the centre of the sponge-like interior, and the king and queen are imprisoned there for life as they are too large to pass through the communicating galleries used by the workers. Grassé has found, in the lower part of these nests, strange pillars which are of a relatively enormous size compared with that of the workers. These pillars are rather like stalactites, for they hang from the roof and do not reach the floor. Their purpose is unknown.

On first examination, the structure of an ants' nest is less striking. One exception is the genus *Camponotus*, a giant ant, which excavates the softest of the annual zones of growth in an old tree stump, to make a series of deep concentric cylinders on to the walls of which the larvae are attached by special hairs. But, in general, ants are content with large nests lacking any regularity as in the case of the untidy heaps of twigs of the wood-ant.[4]

Wasps and bees each have a characteristic honeycomb, angular for the former and round for the latter and the size of the individual cells of the bees' honeycomb is so constant that Réaumur once proposed to use it as a standard of measurement.[5] Very recently Darchen has shown the existence of certain fixed habits amongst bees. A strip of honeycomb which has been introduced at a different angle to the normal seems to upset the bees so much that two teams take hold of it and pull in different directions, to such effect that the strip is quickly brought into conformity with the general pattern. When various other obstacles are found in the comb the bees either remove them or integrate them into the total construction, and it is worth noting that they may try several solutions, rejecting those which are no use.

Social life and caste

The insects in a colony are not identical, although the differences in the case of bees are not very marked. In a bee colony the most important individual is the queen, who is distinguished not for her authority but because she is the egg-laying machine. The queen is fertilised once and for all by 5 to 10 males that die immediately after mating. The number of males or drones raised during the peak season reaches several hundred per colony. All the work is done by the worker-bees, who resemble the queen but are somewhat smaller and have atrophied ovaries. Among the ants, the hierarchy is a little more complicated and, according to the species, there may be one or several queens in each colony, males, workers, and soldiers with enormous mandibles.

Much more varied social stratification is found among the termites. Here the queen is several thousand times bigger than the workers[6] and is accompanied by the king, with whom she mates from time to time, and the soldiers possess curious weapons consisting of an impressive pair of mandibles together with a 'syringe' which pours a sticky secretion over their enemy.

Besides the adult forms, the colony contains young ones at various stages of development and a number of insects in the

---

(1) *It is interesting to note that the bee is the only insect which is bought by the pound. Sometimes silkworms' eggs are also sold by weight.*

(2) *On the subject of 'nectar' see below the paragraph relating to the 'raising of livestock'.*

(3) *P. Grassé states that in many parts of Africa, it is impossible to put a shovel into the soil without unearthing them, and many authors emphasise their role in the formation of humus. Colonies of termites can survive for a very long time, twenty years or more, and Grassé has photographed an African village constructed almost entirely on an ant-hill several yards high whose age must be considerable. Species which construct large ant-hills* (Bellicositermes) *possess gigantic queens (the size of a large sausage, while the workers are no larger than ants) capable of laying a large number of eggs a minute, so that the colony contains several tens of millions of individuals.*

(4) *Regularity in architecture is not necessarily proof of instinctive capabilities. It is of no apparent advantage to the ants, and nothing could be less regular for example, than the plan of our own ancient cities.*

(5) *The dimensions of cells nevertheless show certain variations which make Réaumur's suggestion impracticable.*

(6) *In termites, we find not only female 'workers' but also male 'workers', with atrophied reproductive organs.*

(7) *Very little is known about how the different castes are formed, except in bees. Some recent work has shown that the queen bee secretes a hormone which has the property of arresting the growth of the ovaries of the workers, and this has even been isolated and its chemical formula established.*

(8) *The aphids 'understand' the language of the antennae of the ants, but, so to speak, with their posteriors.*

transitional stages, which precede the division of labour into soldiers and sexual castes. These are capable of replacing sexual adults in case of death or deficiency of numbers. The young termites are mobile in contrast to the passive larvae of bees, wasps and ants.

Differences in the size of the various members of the community are found within the same species, the size varying according to caste, an extreme case being the large termite queen, mentioned above, compared with the workers. In one species of tropical Asian ant, there are two types of worker, one of which is so large that it can carry on its head thirty small workers of the same species.[7]

Exploitation of the environment

As we have seen, the social insects can obtain large quantities of food from their environment. Like men, they are farmers and raise livestock, cultivate mushrooms, and store cereals, meat and sugar, but in some of these activities they face competition. For instance, bees love the honeydew from tree aphids from which they make a dark liquid honey with an odour of fir trees. This honey is considered a delicacy in Germany, where no less than 30,000 tons a year are harvested. In order to obtain a sugary droplet, the ant approaches an aphid from behind, taps two protuberances at the rear with its antennae, and a drop of honeydew falls at once from the aphid's anus. British scientists have noticed that the movements of the ant's antennae during this 'milking' operation are very similar to the way in which an ant taps the antennae of another in order to cause regurgitation of food. Such exchanges of nourishment are common amongst social insects.[8]

Ants not only farm tree aphids but also those of smaller plants. They cultivate them carefully, and when winter comes, the worker ants carry into their nest a supply of aphid eggs which are kept and protected until they hatch in the spring. Then, as the weather improves, the aphids are carried out once more and placed on a suitable plant. At dusk, if the nights are chilly, the aphids are returned to the interior of the ant colony and vigilant 'shepherds' protect them from their enemies, of which there are many. The ants even construct a small shed of beaten earth, in which the aphid offspring are kept under permanent guard and from which they are not allowed to escape.[9]

Unlike bees, ants are incapable of storing sugary matter to be eaten later as and when needed. One species, however, the *Myrmecocytus* of America, has developed a curious biological adaptation. Certain reserve workers act as stores and clinging to the floor of a special chamber they passively receive the sweet juice which is dripped into their gullets by the harvesters. So much is introduced in this way that their abdomens enlarge considerably and may reach the size of a cherry. Later, this stored liquor will be distributed, when necessary, to the famished colony.[10]

Ants are unique in keeping aphids, but they share with termites the art of growing mushrooms. Inside the nests of certain termites, is a spongy mass of decomposing wood full of water and covered with a network of mycelium or spawn, around which the termites work busily. It has frequently been discussed whether the mushroom is actually eaten by the termites, but it would appear that this is not the case although the fungus is the object of very special care and grown from a pure culture. Its function seems to be to predigest the wood and doubtless to enrich it with many nutritive factors which make it more suitable for the termite.

The *Atta*, the mushroom ants of South America, cultivate mushrooms in quite a different way in underground plots extending over several square yards. Beds of decomposing leaves are carefully sown with one particular species of fungus for each species of *Atta*, and the mushroom provides grazing for the colony.[11]

The harvesting of grain

Another type of ant, the *Messor*, harvests seeds of a herb, which is sometimes known as ants' 'wheat' and it has been supposed that these ants actually sow their favourite plant, since it is often found growing around their nests. However, the clumps are not intentionally planted but are merely the result of accidental germination of seeds which have fallen during the harvest. The ants crush these seeds and make a kind of paste, which they then put in the sun to dry and later distribute it to the larvae.

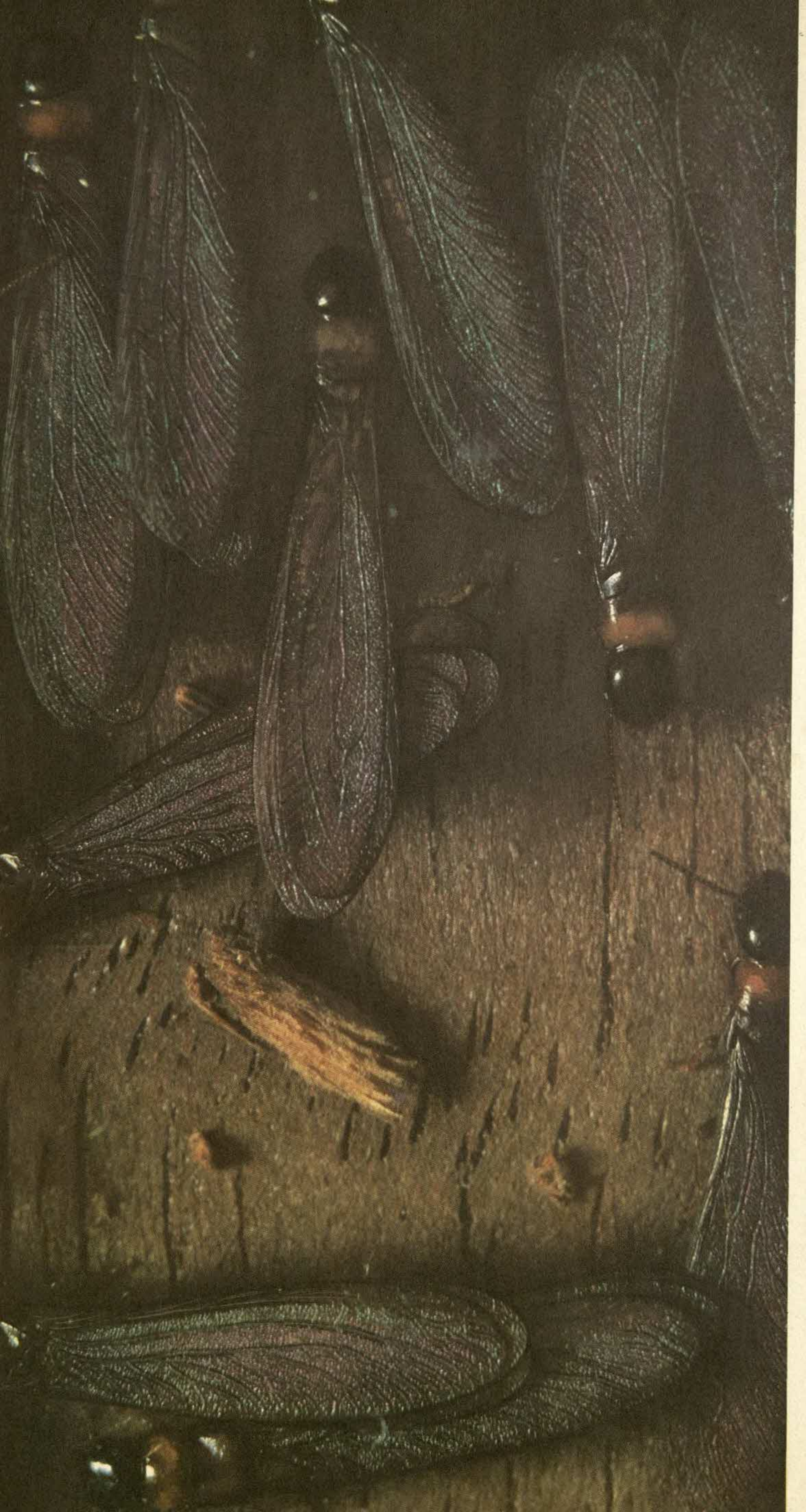
Certain American wasps, the Polybiinae (which construct the enormous nests mentioned above), harvest not only honey, which is unusual for wasps as they are generally carnivorous, but also dead prey which is arranged in the nest on shelves specially provided for the purpose. How the prey is preserved is not known, though it has recently been discovered that there is a whole series of antibiotics in use among social insects some of which act both against fungi and to prevent

The entrance of the hive, with some ordinary coming-and-going. In the lower part of the picture a bee is ventilating the hive with its wings while the others return charged with pollen. (Photo Lod).

(9) *Their love of aphids is not exclusive. Certain species in addition raise cochineal-beetles which also produce a sugary liquid.*

(10) *The cherry-shaped ants filled with honey are a delicacy sought for by the Indians. The skin of the ant forms a very thin covering over the honey.*

(11) *The* Atta *are so concerned with their mushrooms that they do not hesitate to defoliate a whole orchard in order to make a large enough bed for them. They are a pest against which as yet no remedy is known.*



Termites belong to the group Isoptera, *a primitive order of insects which leave the egg in a form very similar to that of the adult. Almost all termites live in tropical or subtropical zones. Among these social insects, the neuters are dedicated to the work of the colony. Their communal organisation is always based on the 'royal couple', a queen accompanied by a male which has fertilised her (middle picture, below). The various castes are determined by heredity and not by differences of diet, as in bees. The picture on the left shows some young termites (imagos). These pigmented reproductory individuals are the only forms able to tolerate daylight. They are originally winged, but shed their wings, like the queen ant, on their return to earth, after they have accomplished their one and only flight. The soldiers (middle picture, above) are wingless. Their heads and their mandibles are enormous, proof of their defensive role. Living a subterranean existence, they have degenerate eyes. The workers (right) are whitish, unpigmented, and wingless. Their eyes are rudimentary. They are responsible for the construction of the nest and the collection and storage of the food, serving the needs of the other castes. (Enlarged 15 to 30 times, Photo Lod).*

germination. Such insects smear the antibiotic around the interior of the nest in order to protect it against mildew and bacterial attack, so it is possible that the Polybiinae use antibiotics to keep the contents of their larder fresh.

War and slavery

Bees are normally peaceable but, when scarcity threatens, the stronger colonies do not hesitate to massacre the weaker and pillage their food-stores. Termites appear to be even more peace-loving, but too little is known about them or the wasps to judge their prowess as warriors. Ants, on the other hand, have specialised in warfare. Thus the large 'stink ant' of Africa[12] lives only to persecute unfortunate termites: a scout locates neighbouring colonies and after returning to its nest returns with a large escort which it leads into battle. In contrast to bees, which have a highly organised language, no message appears to be passed from one individual to another. The squad is simply alerted and follows the scout and, if the scout is removed the disorientated ants spread out in all directions. If it is put back once more the procession re-forms quickly and purposefully and the termites rarely offer any resistance to these enormous ants.

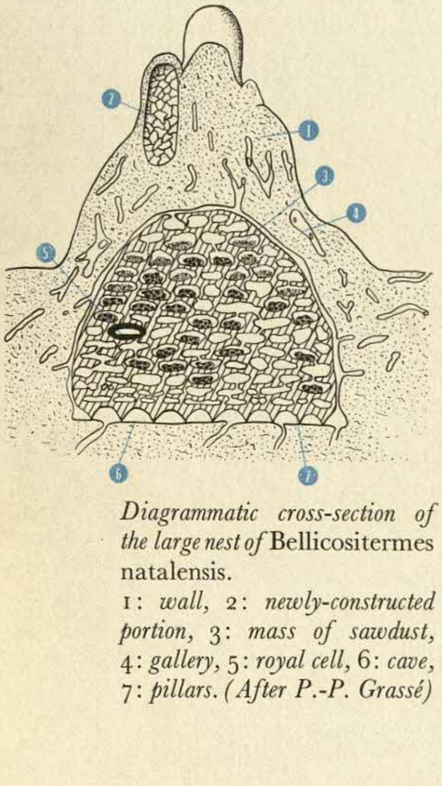
Even among various species of ants warfare takes place, mainly in order to procure slaves. Several species, such as the blood ant, or *Polyergus*, attack, in a disciplined way, the ant-hills of other groups, such as *Formica fusca*, massacre the workers and carry back the young larvae which, when reared, faithfully serve their new masters.[13]

'Vice' amongst the social insects

Both ants and termites are infested by a considerable number of parasites[14] which grow fat at their expense, often behave viciously and yet seem to be tolerated. Why this is so is not known, although we have certain clues: for example, in many instances the parasites possess trichomes or hairs which secrete a liquid of which the ants or termites are very fond. In the case of ants Wassmann has made a study of *Lomechusa*, rove-beetles (Staphilinidae), which parasitise ants. When these penetrate into the ants' nest, the colony is doomed, because the parasite puts its own larvae with those of the inhabitants and, as the beetle larvae grow, they are tended by the ants as if they were their own. The beetle larvae, which grow legs, while the ant larvae have none, even go to the extent of deceiving their hosts by folding them up and in the course of time they eventually devour the young ants growing at their side, while the naive nurses are not looking. During this period, the adult rove-beetles secrete a liquid which the ants swallow and show all the symptoms of intoxication: they struggle and stumble wildly along the length of the galleries, neglecting their larvae which thus give rise to degenerate and useless workers. Soon the colony is destroyed, killed by the beverage produced by the rove-beetles. This is one of those very rare cases where animals drink themselves to death.

The social organism

Many writers, amongst whom I am one, believe that the colonies of social insects should be regarded as a kind of super-organism, the individual members of which are, in effect, free-roving cells, unable to live for long away from the social body. This is certainly true of ants, termites and bees which cannot live in isolation and die in a few hours when they are separated from their group. Further, all of these insects, whether in the isolated state or in small groups, are quite incapable of any complex activity and only when they are together in the community or super-organism does their typical pattern of complex behaviour emerge. The super-organism can be compared with the ordinary multicellular organisms whose cells are less mobile. For instance, the super-organism is controlled by hormones circulated by the continual exchange of regurgitated food. We are fairly sure that this social circulation exists, and even know how to measure it. Moreover, the super-organism has its reproductive organs, in the form of the queen and the males, and perhaps even a collective nervous system which consists (as in large electronic machines) of an interconnection of multiple elements that, in themselves, have only very limited possibilities.



Diagrammatic cross-section of the large nest of Bellicositermes natalensis.
1: *wall*, 2: *newly-constructed portion*, 3: *mass of sawdust*, 4: *gallery*, 5: *royal cell*, 6: *cave*, 7: *pillars*. *(After P.-P. Grassé)*

---

(12) *The 'stink ant' is an African species. They produce such an unpleasant smell that a single individual, if crushed, makes a room uninhabitable for an hour or two.*

(13) *Certainly they have an excuse: their long thin mandibles are useful only for fighting and not for work, so that slavery is really a necessity.*

(14) *There are hundreds of species of insects which live as parasites in the termites' homes or in ant-hills.*

Camouflage, warning, and disguise

Leendert de RUITER

To many animals the hazards of life under natural conditions are almost overwhelming; few live to feel the burden of old age. The odds against the robin that sings at this moment surviving for one more year are about three to two. In other words, the average age reached by these birds in the wild is less than two years, though in captivity they may live for more than ten. The fate of many other birds and mammals is the same, and invertebrates often seem even worse off.

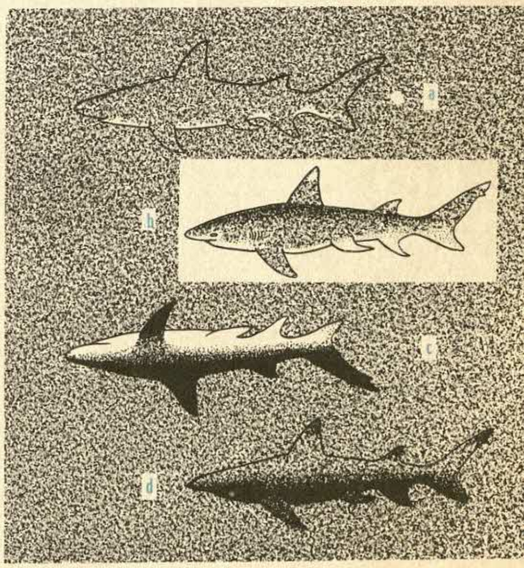
To be sure, some species are known in which the majority of individuals are granted a large share of their potential lifespan. Yet as a rule the rigours of life in nature are extreme.

This has an important consequence. The whole structure and constitution of all animals is perpetually put to the test. In the millions of years of life's history this has moulded each detail of their bodies into the shape best suited to meet the hardships of the environment, or at least into the best shape attainable in the given circumstances at the given time. That we have grown aware of this is perhaps the most important development in biology during the past hundred years. It will never do to dismiss even the most bizarre forms of life as mere sports of a wanton Nature. Nor must we overlook the fact that even those types of organisation which are so commonplace that we hardly notice their existence, may well be there for a good reason. It is always worth while investigating whether and how each detail of structure is useful to its owner. Animal colours and patterns are no exception.

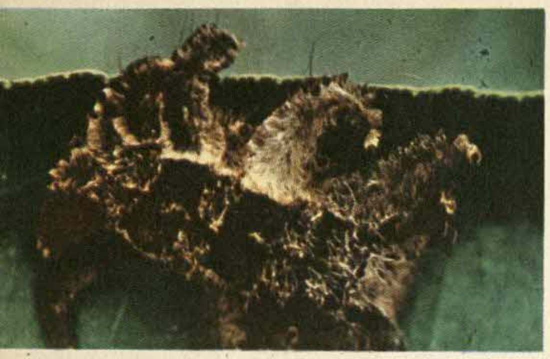
Let us consider some facts. One, so common that we fail to notice it in everyday life, is that many animals closely match the colour of their environment. It is only when startled by the pheasant, flying up from almost under our feet, that we realise this, but it can be seen equally well in the dull brownish tinges of most of the small creatures crawling among the dead leaves on the forest floor, in the fauna of fresh water and the sea—whether free-swimming, or in the creatures attached to the bottom, of deserts and tropical forests as well as those which populate the arctic snowfields.

These resemblances require explanation. In less than one in a thousand cases are they due to actual pigments from the environment, taken up with the food. Nearly always the environment is without direct effect; for even when reared in an abnormally coloured habitat, the animal will develop its typical pigmentation. There are two groups of exceptions to this rule. In a few cases such as some caterpillars, grasshoppers, and waterbugs, the colours of the background are registered by the developing insect, and its processes of pigment formation regulated accordingly, so that the adult will match whatever environment the larva was given. Secondly, many fishes, amphibians, reptiles, squids and crustaceans, can actively change colour by contracting and expanding their chromatophores, which are cells in the body wall containing the various pigments. Throughout their lives, they can adapt to the colour of their background within a few minutes. Of course, neither of these phenomena entitles us to regard similar colour as a pure mechanical effect of environment.

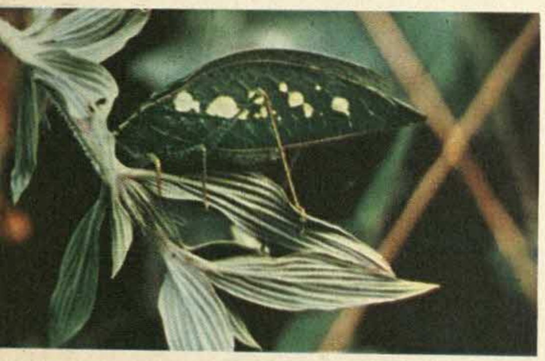
A better explanation was put forward more than a century ago: colour resemblance serves as a camouflage, hiding animals from the eyes of their natural enemies. Most of the direct evidence for this view, however, is much more recent. It was obtained in experiments such as those of Popham, who put adult waterbugs (*Arctocorisa distincta*) into tanks with sand-covered bottoms. Some of the bugs matched the colour of the sand perfectly, others less well. He then added one or more minnows—natural enemies of the bug—and watched what happened, taking scrupulous care, as one must always do in such work, not to disturb the normal behaviour of either predator or prey. He found that many more victims (up to about six times) fell among the contrasting bugs than among the better-



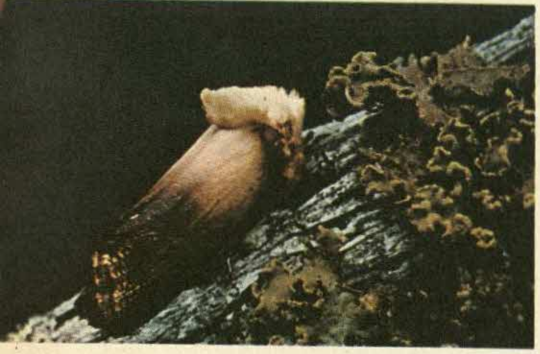
Principle of counter-colouration. In (a) all the parts of the shark have the same tone as the background. In (b) the back is darker and the belly lighter than the background: the shark is only visible when it turns on its back. (c) Shows how, in the same way, light or shade and colour combine together to annul each other. In (d) we see the normal pigmentation of the shark in the absence of any shade.



This larva of Phoebetron *(one of the nocturnal Lepidoptera, or moths) demonstrates a striking example of mimicry: it protects itself against its foes by imitating a spider with an unpleasant taste as the birds well know. (Mag. × 2. Photo Kettlewell).*



This specimen of the Orthoptera (Phylloptera) *shows a striking example of camouflage: it imitates a leaf with spots of mould. (Natural size. Photo Kettlewell).*



Cossula notodontoides Shaus. *Another extraordinary example of camouflage: this Brazilian butterfly imitates a fallen flower. (Specimen slightly enlarged. Photo Kettlewell).*

adapted ones. The greater the contrast, the greater the risk. Ergene, working with grasshoppers hunted by chameleons or birds, got analogous results. Sumner kept hundreds of small fish (*Gambusia patruelis*) in white and black tanks until they had fully adapted their pigmentation. Then he brought together equal numbers of the two groups in either a dark or a light-walled tank. Predatory sunfish, penguin or night heron, when introduced into the aquarium, caught about twice as many of the contrasting as of the adapted specimens. Such results leave no doubt that the adjustment, in the course of the individual's life, of its colour to its background, may often be a great help against natural enemies.

It is more difficult to get sound proof of the value of colour resemblance in animals whose pigmentation cannot be modified during development; for how can a standard for comparison be found? The logical standard is the ancestral form which lives in the same environment, but has not yet acquired the present colouration of the species. This is rarely available but we have one beautiful example.

In the industrial areas of many countries, a fascinating change has occurred in many moths (in England about seventy species in all) since the middle of the nineteenth century. One species after another has become melanistic (darkly pigmented), whereas the same species in rural areas has retained the ancestral pattern. The difference between the two forms is hereditary. In fact, 'industrial melanism' is nothing less than a process of evolution, taking place under our very eyes. Kettlewell availed himself of this opportunity, and studied a classical example of industrial melanism, the Peppered Moth. He released many hundreds of marked specimens of both the black and the normal moths, in rural as well as in industrial areas, and investigated what happened to them. The results proved definitely that in the country the mottled grey of the normal moths gives them good camouflage on the lichen-covered tree trunks where they spend their days whereas birds found the black specimens much more rapidly. No lichen, however, can grow in the polluted air of industrial districts, and he showed beyond doubt that here, on the bare trunks, the black moths are better protected.

In addition, it has long been known that the caterpillars of the black form, though outwardly normal, are more hardy under adverse circumstances than those of the grey type. For both reasons, black moths in industrial areas will, on the average, leave something like a third to a half as many offspring as grey ones. This provides a simple and quantitatively adequate explanation of the rapid *spread* of industrial melanism. Of course, it does not explain its original *appearance* which must have been due to mutation.

This is the best case where we have practically complete proof that natural selection or survival of the fittest, as postulated by Darwin, is the driving force behind evolutionary processes. A good deal of more fragmentary evidence to the same effect might be produced for all other types of adaptive colouration and, in fact, the study of adaptive colour patterns has provided strong support for the neo-Darwinian theory of evolution which has been gaining ground for the past thirty years.

It is only recently that we have become aware of the fierce intensity at which natural selection may operate. To assess this, it is not enough to know that of two competing forms one runs, say, half as much risk from a given danger as the other; we must also know the absolute magnitude of this risk, for if it is only slight, little can be gained by halving it. As regards the risk from predatory foes, ecological research shows that this is often high in natural populations. In a single month in spring, an average of one in twelve of the sparrows in a given rural area was killed by sparrow-hawks year after year. From a third to a half of the *Panolis* caterpillars in a pine wood are eaten by songbirds during the brief period when they are big enough to attract the birds. Of the cockles in a mudflat, 22% were killed in one winter by oyster-catchers alone, who thereby accounted for about a third of the cockles' total losses. Such figures indicate that anything which materially lessens the risk of predation, as does colour resemblance, must be greatly favoured in the struggle for life.

Camouflage

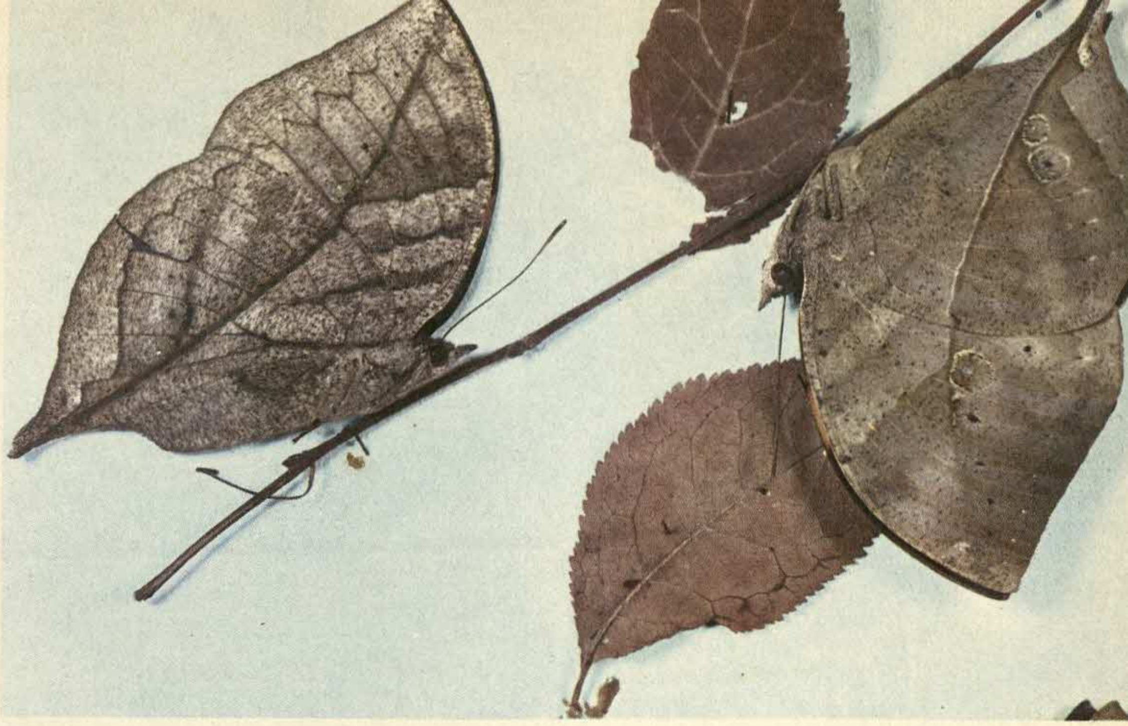
Nevertheless, simple colour resemblances cannot make an animal immune from its enemies. There are several reasons for this, the most obvious one being that camouflage can only deceive the eye, not the other senses of the enemy, which may find its prey by smelling it or even by accidental contact. Further, most natural environments are not homogeneous, so that no complete match is possible, and we have seen that some animals meet this difficulty by changing their colours when necessary. Many others, lacking such powers, solve the problem by always selecting that part of the environment which best suits their own colours. This was demonstrated, for example, by Popham and Kettlewell with their waterbugs and moths, respectively. Indeed in any case of adaptive coloration, be it camouflage or advertisement, we always find the behaviour of the animal in such harmony with its colour and pattern that the adjustment is invariably presented to the best advantage.

There is another reason why colour resemblance alone gives imperfect camouflage: a uniformly coloured body, seen against a background of the same colour, is still conspicuous because of the gradations of light and shade on its surface. However, as Thayer has pointed out, this can be avoided by making the upper side darker and the lower parts lighter in tone just as much as is necessary to compensate for the gradation in light intensity. Shade is an important recognition mark of solid objects to man and probably to most animals and a body thus 'counter-shaded' will merge completely with a background of the same colour.

Graded pigmentation is so common in nature that anyone can think of dozens of examples: in mammals, birds, reptiles, amphibians, fishes, insects and other invertebrates. Is all this really countershading? One point certainly seems to confirm that it is: almost all these animals turn their dark side to the light, as is required for the gradation to have a concealing effect, the only exception being cases in which we know, from other evidence, that the patterns aim at advertisement rather than camouflage as described later. This striking correlation between habits and pattern is found even in such groups as the caterpillars, where the gradation may have almost any direction (back to belly, belly to back, head to tail, tail to head), a fact that seems harder to understand unless concealment is the function of the gradation. Some direct evidence was obtained by the present author in experiments with birds hunting countershaded caterpillars. The results indicate that countershading may contribute to camouflage nearly as much as the colour resemblances discussed above.

Disguise

We, ourselves, do not see an animal merely as a patch of colour—we also perceive its shape. Of the way in which animals recognise their prey far too little is known as yet, but there is no doubt that here, too, shape is important. Hence, in spite of concealing colour and countershading, the prey risks betraying itself by presenting a tell-tale outline. To avoid, this, some animals have actually disguised their shape in the course of evolution, for example, seaweed-like fishes or twig-shaped caterpillars. In most of these cases the animal has taken the shape of some common object of no interest to its enemies—a leaf, a twig, or a stone. The advantage is obvious.



There is some evidence (for instance, from experiments by the author with birds searching for stick caterpillars) that high perfection in these disguises is an important factor in natural selection. A bird that has by sheer luck found a stick caterpillar, but cannot tell these larvae from real twigs, may go on picking up such objects for a while. It will soon be discouraged, however, because there are far more twigs than larvae, as the members of a camouflaged species always live widely scattered. If, on the other hand, the bird can notice a difference, it will start hunting specifically for the larvae, whose camouflage then helps much less. This in fact is what happens in nature: once a prey becomes so abundant that chance encounters occur frequently, the predator learns to see through its camouflage, and can then greatly intensify its pursuit. Tinbergen has argued that, in complex natural communities, such processes may even help to stabilise population densities of prey species. However, actual distortion of the body outline for the sake of disguise will rarely be feasible, since the shape of the body must also fulfill other requirements such as those of locomotion. Here, as everywhere in evolution, a compromise is struck between conflicting demands. This may be the reason why disguise of structure is so often achieved by purely 'pictorial' means, by pigmentation and patterning that hold the eye and distract it from the meaningful forms.

The butterfly, Kallyma inachis, of Assam, imitates dead leaves even to the point of reproducing the moulds which grow on them. Below, the back of the butterfly, showing lack of camouflage. (Photo Lod, with thanks to M. E. Le Moult).

HISTORICAL NOTES

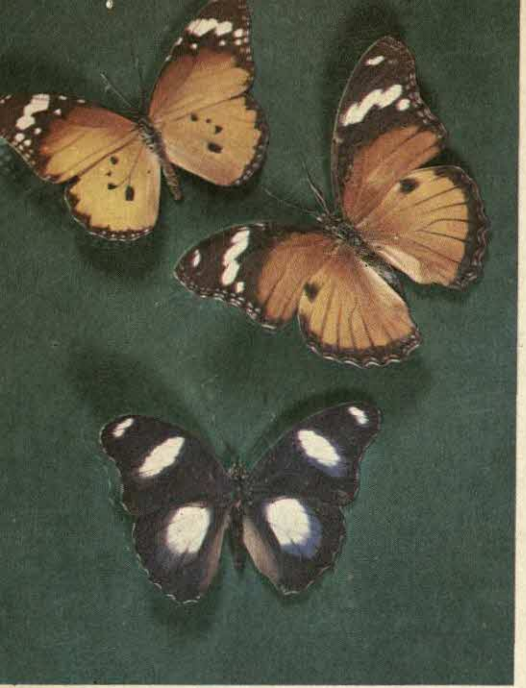
1861

H. W. BATES discovered the type of mimicry in which an edible species of insect mimics an unpalatable species.

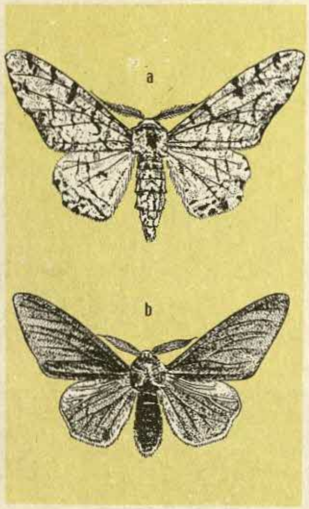
1877

FRITZ MÜLLER discovered the type of mimicry in which a number of species of unpalatable insects mimic each other and thereby share the losses incurred by them all from the attacks of predators.

Continued on next page



This butterfly (Hypolimnas misippus) *is doubly remarkable: the female (above) mimics an entirely different species (centre) which is avoided by birds on account of its unpleasant odour; the male (below) shows a striking sexual dimorphism, and one might almost take it for another species.*



(a) normal, and (b) melanistic specimens of the Peppered Moth (Biston betularia).

Continued from previous page

1936

E. B. FORD demonstrated the reality of the protection afforded to Batesian mimics by showing the degree of perfection in the mimic's resemblance to the model depends on the numerical preponderance of models in the same habitat with the mimics.

Patterns of camouflage

Many insect larvae live on the shoots of pine trees and, whatever their colour, they will risk being conspicuous by reason of their size among the slender needles. But some of these species have independently hit upon the same solution to this problem: they wear a pattern of green longitudinal stripes, about the same colour and shape as pine needles, separated by white bands, and one need only have searched for these larvae in the field to appreciate how effective this camouflage really is. It is interesting to note that such patterns are found in quite unrelated groups, such as moths, sawflies, and flies. Moreover, on close inspection the methods employed differ from one case to another, even within the same group. The white bands may be located in the live tissue of the skin, or they may be due to a waxy layer on the cuticle; the green pigment may lie in the skin, blood, or gut, or in a combination of these. The impression one gets is that it was the result that mattered, and that every species has quickly utilised whatever means came to hand. Such 'convergences' are often found in the patterns of animals inhabiting the same habitat and indicate that they must have some vital function. Indeed, field observations by Tinbergen and his colleagues, and experiments with birds made by the present author, have shown that the striped patterns of the pine insects are very good camouflage although, as we have already seen, they are less effective against searching by experienced birds.

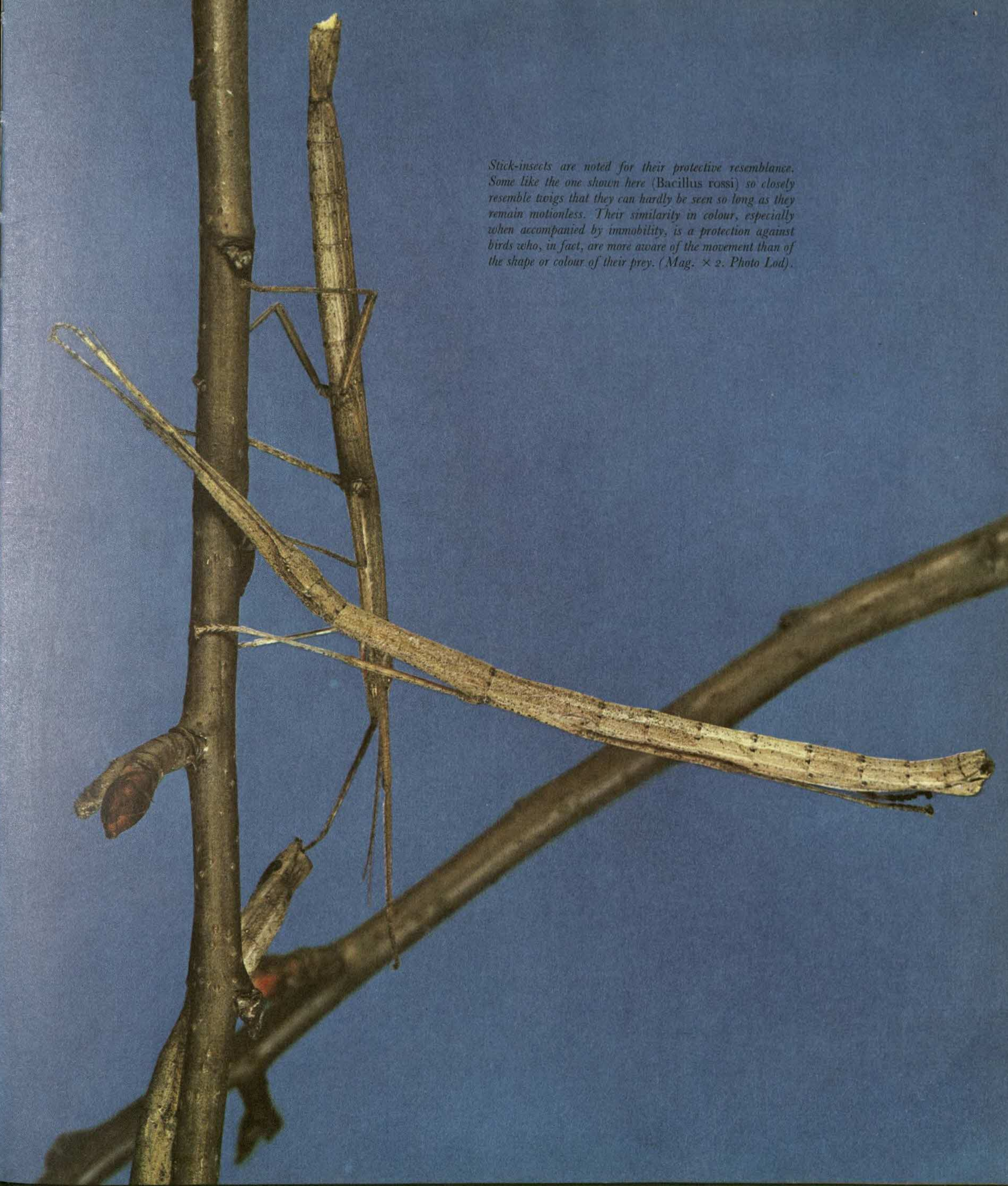
Disguise by patterning, like actual modification of shape, is most effective when it makes for resemblance to some common or uninteresting object. This does not always require such a well-defined pattern as the stripes of the pine insects. Many animals live against irregular backgrounds, such as dry leaves, tall plants, or on a pebbled beach and beautiful camouflange can then be achieved by simple patterns of irregular spots. In such designs, colours that also occur in the background are usually brought side by side in bold contrast, often enhanced by the fact that towards the boundaries between dark and light the dark patches become still darker, the light areas lighter. The main features of such 'disruptive' patterns usually show a complete disregard of anatomical boundaries in the body, and may run at right angles to its outline.

There seems to be no experimental proof of the concealing function of disruptive markings, but there is a good deal of circumstantial evidence. Simple experiments on man's perception convince us that such patterns distract our attention from the outline of an animal. Is it safe to assume that its natural enemies will be baffled in the same way as we? A certain amount of work has been done on the way predators make use of the colour, shadow, or movement of their prey as recognition marks. There are, of course, wide differences among species, for instance in colour vision, and much more extensive studies are needed. As far as they go, however, the results to date suggest that features known to conceal an animal from the human eye will often have similar effects on its natural enemies, though not necessarily to the same degree. If we add the phenomena of convergence (see above), and of adaptive radiation (when related species differ in pattern, each having developed in harmony with its environment), we may feel safe in ascribing a concealing function to these disruptive patterns.

Nevertheless, of all European pine insects, less than one fifth wear a striped pattern. Why is this so? Obviously because the ultimate problem for each species is not how to conceal itself, nor even how to reduce predation pressure, but quite generally how to survive in spite of its predators and all other dangers. The species may turn the scales in its favour just as well by raising its fecundity, or lowering its susceptibility to disease, as by evading its predators, though here we must restrict ourselves to the latter aspect. Even for that, however, there are other means than a striped pattern. Some pine insects, such as the larvae of *Lymantria*, although feeding on the needles, spend most of the time on the rough brownish bark of twig or trunk, and are coloured accordingly. This is specially striking in the Pine Hawk larva, which exchanges its green stripes for a mottled brown pattern when it grows too big to rest among the needles.

Other pine insects do not try to hide at all. The larvae of the sawfly *Diprion pini* live in clumps of dozens of pale yellow individuals visible from afar and when disturbed perform jerking movements which make then even more conspicuous. Yet Tinbergen and his co-workers found that a *Diprion* larva runs one thousand times less risk of being killed by a bird than does the beautifully camouflaged *Panolis* caterpillar. Prop has shown that the sawfly owes its immunity to resinous substances in its gut, which make it unpalatable to birds.

The notion that predation depends on palatability as much as on visibility is not new. Half a century ago Swynnerton, by means of



Stick-insects are noted for their protective resemblance. Some like the one shown here (Bacillus rossi) *so closely resemble twigs that they can hardly be seen so long as they remain motionless. Their similarity in colour, especially when accompanied by immobility, is a protection against birds who, in fact, are more aware of the movement than of the shape or colour of their prey. (Mag. × 2. Photo Lod).*

a vast series of experiments, proved:

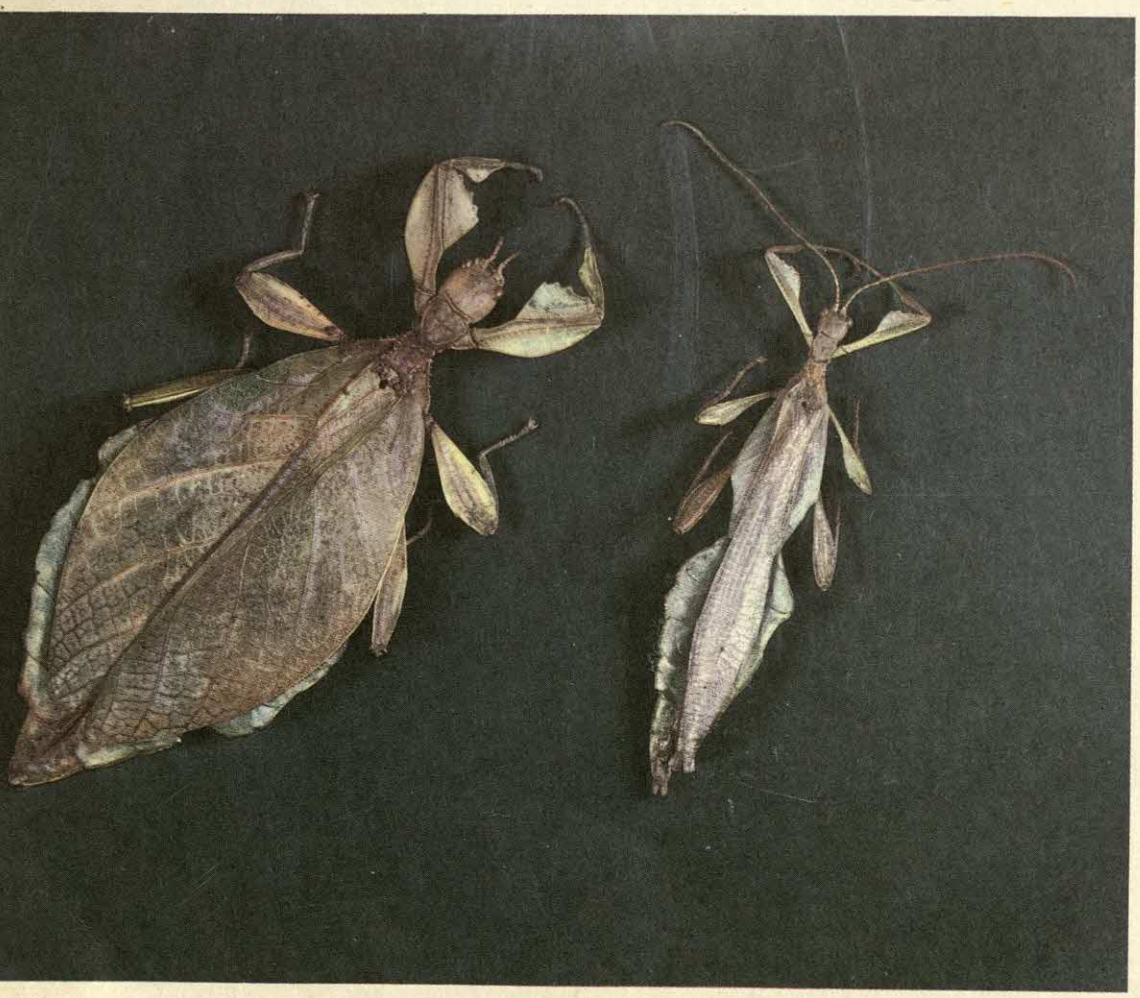
1. Birds have a finely graded appreciation of the taste of their prey and how far down the scale a bird will go at a given moment depends on its hunger: the more hungry the less finicky.

2. Experienced birds know their prey by sight, and need not taste them to judge their acceptability. It follows at once that a species which tastes so unpleasant as to be almost never accepted simply need not trouble to hide.

Fair fowl are foul fare

However, this cannot be the whole story, for the patterns of unpalatable prey show no mere absence of camouflage. They tend to be positively conspicuous and this has to be explained. Hale Carpenter, working in Africa, found that of the prey rejected by his monkeys no less than 87% were conspicuous by their pattern and habits (as opposed to 21% of the more palatable prey). Indeed, we are all accustomed to associate bold patterns with unpleasant properties—the wasp and its sting, for instance. After many tests, in which his fellow officers, cats and hornets acted as predators, Cott concluded that 'fair fowl are foul fare'. Distastefulness in the animal world is often combined with conspicuousness.

The Leaf Insect (Phyllium siccifolium) *of Java imitates a green leaf to perfection. Female on the left, male on the right. The size and shape of the male provides another excellent example of sexual dimorphism. (Photo Lod, with kind permission of M. E. Le Moult).*



Lloyd Morgan, studying the feeding behaviour of domestic chicks about 1890, discovered what lies behind this. Newly hatched chicks will peck at almost anything and each must learn individually what is edible and what is not. Other work on birds, amphibians and fishes, has given similar results. In general, there appears to be little 'instinctive' knowledge of food; for even the least edible prey is not safe from the inexperienced predator. For such prey, therefore, it is vitally important to reduce the number of mistakes its enemies make: they must look *different* from the common run of edible prey, which as a rule must be rather inconspicuous. Surely, their mere being different is one advantage of these so-called warning or aposematic patterns of unpalatable prey. Another favourable effect may be that, of all 'different' patterns, it is the more conspicuous ones that are memorised more rapidly and retained longer, but one might wish for more experiments on natural predators to prove this point. If we add, for instance, that conspicuous patterns usually go together with exposed, sluggish, and often gregarious behaviour, and that in winter—when food is so scarce that even the least edible are in danger—conspicuous patterns are rare, we can hardly doubt the function of warning coloration.

It is clearly impossible to divide all patterns into two distinct classes, conspicuous and concealing. There is a large intermediate group, and Prop has suggested that only a very distasteful species can brave its predators at all times. Those of intermediate palatibility cannot afford more than moderately distinctive markings, which will serve to remind the predator of their poor taste when food is ample, without making them fatally conspicuous in periods when hunger overrules the predator's fastidiousness. The most palatable species, of course, are well advised to remain in hiding at all times. The fact that in the genus *Diprion*, and probably in other cases as well, the conspicuousness of the species is inversely related to their palatability, certainly supports Prop's views.

Conspicuousness and mimicry

Conspicuous species present yet another problem: several of them, living together in the same area, sometimes have surprisingly similar patterns, although they are not in any way related. One possible function of such mutual resemblance was suggested by Fritz Müller: inexperienced predators attack prey they will later leave unharmed. If several of the species involved seem deceptively similar to the predator, he will learn to avoid them all at the same time, so that they can jointly contribute to the cost of the predator's apprenticeship, each severally being taxed much less than if it were alone. This is now called synaposematic colouration, or Müllerian mimicry.

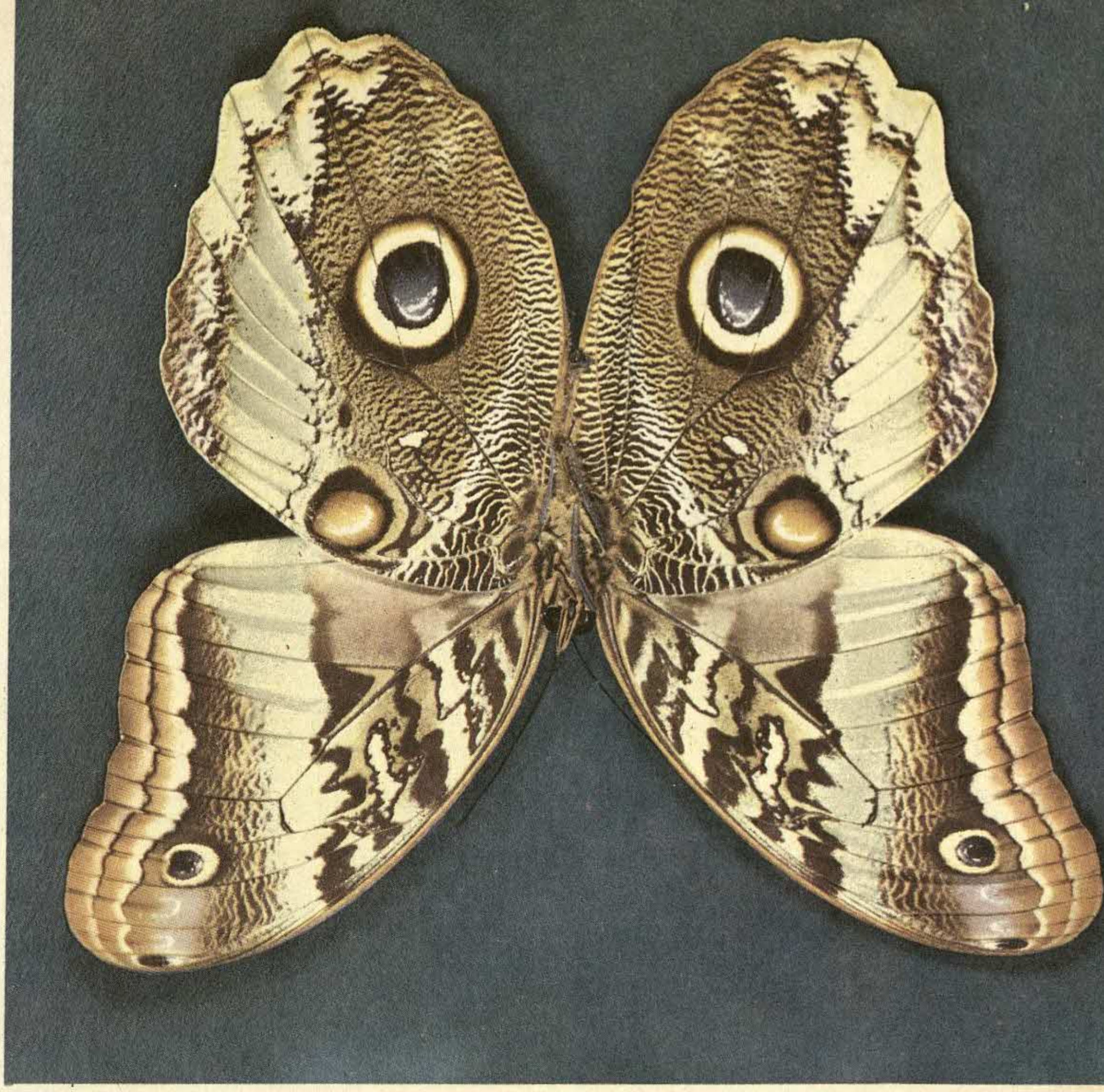
Often, however, of two species resembling each other only one is unpalatable, the other edible. A different explanation is then required. This was given by Bates as early as 1861: if the two species are practically indistinguishable to their enemies, and if the edible form (the 'mimic') is much rarer than the distasteful type (the 'model'), predators will be discouraged from attacking such prey, and the mimic will owe to its disguise the benefit of its model's unpalatability. This is known as Batesian mimicry.

An endless number of mimetic resemblances have been described. Some are the product of fancy rather than fact, but many are genuine. The most familiar case in temperate climates is the imitation of wasps, bumble-bees and bees by hoverflies and moths. Mostler has proved that this is true Batesian mimicry: birds will eat the hoverflies with relish, until they have had unpleasant experiences with wasps. From then on they will rarely touch either hoverfly or wasp. But the best example of mimicry are found among butterflies, and for a few of these L. and J. Brower have shown in tests with birds that here, too, the Batesian principle is operating. In many other cases, indirect evidence leads to the same conclusion. For example, mimics very rarely occur outside their models' range of distribution, and mimics are always rarer than their models; the resemblances prove to be due to convergence, and mimics imitate, not only the colours, but also the movements of their models.

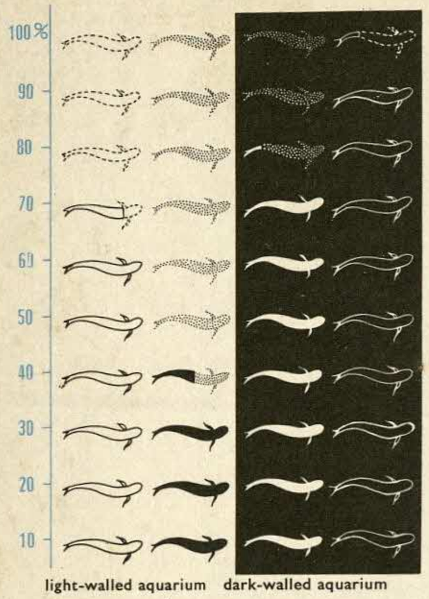
False pretences

In practice, the boundary between Batesian and Müllerian mimicry must be vague. No two species will ever be of exactly the same palatability and as long as food is plentiful, both members of a mimetic pair may be rejected because of their taste (Müllerian mimicry), but with increasing food scarcity, the better of the two may in itself become acceptable, and merely be protected by its resemblance to the other (Batesian mimicry).

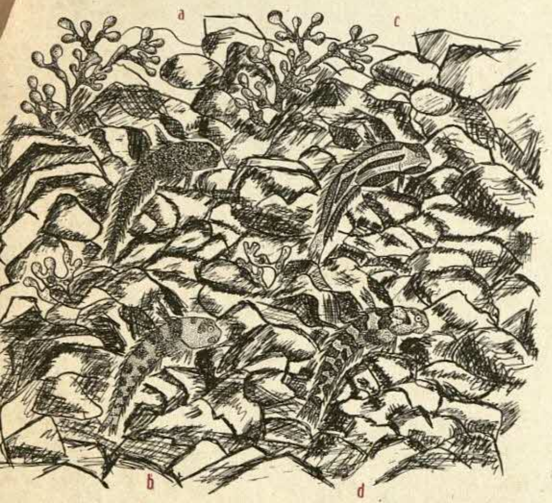
In principle, however, the distinction is very important, for in the Batesian case we meet with a new phenomenon: that of a species protecting itself by inspiring avoidance in the predator *on false pretences*. This is called 'false warning' or pseudaposematic colouration. Such defence by bluff is not uncommon, but it has a serious drawback: an enemy who has once seen through the façade will soon lose all respect for the fierce appearance of that prey. Therefore, with the exception of Batesian mimicry (where the model reinforces the predator's respect), such bluff is usually employed as a last-line defence by camouflaged species: if found in spite of their concealment, they flash into the face of the enemy a startling pattern (often previously hidden), sometimes only a bright colour, as on the hindwings of many moths, sometimes an elaborate pattern.



Certain butterflies, like this Calligo atreus, *show on the underside 'eyes' which imitate the head of an owl. This forms a useful means of defence; for, by spreading their wings, they are able to scare away not only predatory birds but even insectivorous monkeys. (Photo Lod, with kind permission of M. E. Le Moult).*



Experiment by Sumner on the fish Gambusia patruelis. From above down: percentage of survivors. The dotted parts indicate the number of animals killed by the sunfish.



The principle of disruptive camouflage: an attempt at camouflage based on the simple mingling of tints (a) is improved by contrasting patterns (b) particularly when the contrasts are vivid (d) and the patterns arranged at right-angles to the length of the animal. (Compare c and d).

In particular, 'eye-spots' are often used, that is, concentric colour markings which typically consist of rings suggesting a light 'iris' and a dark 'pupil' (of course, eye-spots have nothing to do with real eyes). Blest has shown that the sudden appearance of almost any contrasting pattern frightens birds, but that eye-spots, especially the very eye-like markings of insects, are the most effective in deterring avian predators.

Adaptive colouration

So far we have only considered how adaptive colouration may help prey to escape their predators and this alone provides a vast field of study. Yet the patterns of animals have many other functions as well. Camouflage is just as valuable to the predator creeping up on its prey, as to the prey itself. Colour resemblance, countershading, and disruptive patterning, as seen in defenceless prey, occur just as much in the patterns of lions, tigers, sharks, etc. A good many predators, otherwise camouflaged, even lure their prey towards them by displaying coloured structures resembling its food, such as the wriggling worm-like appendages on the jaws of some turtles and fishes.

Moreover, the functions of colour patterns range beyond the relations between predator and prey; for they are just as important in intraspecific communication. They play a role in threat (the hood of the Black-headed Gull) and appeasement (the white crest of the Night Heron), in courtship (the nuptial colours of birds, fishes, cuttlefish) and parental care (the coloured inside of the mouth of nestling songbirds gaping for food), in species recognition (the wing specula of ducks) and in keeping the herd together (tail markings of deer). The function of all these patterns is to signal the identity and intentions of their owners to fellow members of the species. They must, therefore, be clearly visible, and it is understandable that conspicuousness is achieved in the same ways here as in warning patterns. These ways, varied as they are, can all be regarded as the exact negation of the principles of camouflage: we see bright contrasting colours combined with striking display movements; countershading is discarded, as in the male stickleback's nuptial dress, or even becomes inverted, and so on.

The exact function of many intraspecific demonstrative patterns has been revealed by behaviour studies, but we know little of their quantitative importance in the struggle for life. Such information is more difficult to get in this field than in the case of adaptations against predators, for it is easier to determine the risk that a prey will be killed, than to assess the subtle effects of intraspecific signals on the descendants of an animal.

Perhaps the best analysis so far of intraspecific demonstration is that of the colour of the herring gull's bill made by Tinbergen and his associates. The gull chick begs for food by pecking at its parent's bill, which is yellow with a red patch near the tip. Chicks will also peck at artificial models of a gull's head. Thus we can analyse which features are the most important. Shape, size and colour of the parent's head proved immaterial, but the attractiveness of the bill was enhanced by its elongated shape, lowered position, and particularly by the presence of a contrasting patch, preferably red. The investigators were even able to construct an 'improved' gull's bill, a red pencil-shaped rod with white rings at the tip. The chicks would peck more readily at this than at a model of a normal gull's head. Thus a gull with such a bill would find it easy to get its young to feed, but whether future evolution will produce gulls with such bills remains to be seen; for they would seem hardly suited to most of its other uses.

To summarise, the following picture seems to emerge. Every animal in Nature is watched by others, by members of the same and of other species. Many of the latter may either harm or help the animal observed, but what they do depends on the nature of the signals they receive. Through aeons of evolution, therefore, natural selection has worked on the colour patterns of all animals to suppress those messages that would induce inimical behaviour in others, and to enhance the signals giving rise to advantageous reactions in the animals seeing the patterns.

The result is a limitless number of fascinating adaptations in which colour, pattern, the shape of the body, and behaviour cooperate in perfect harmony. I have tried to illustrate this by a few examples, mainly chosen from recent work which has not yet been summarised in all handbooks and with some bias for cases I know of from personal experience. Yet, wonderful though the phenomena of adaptive colouration can often be, we must bear in mind that they are only one of the means of survival, the importance of which to any species can be assessed only when we know what other defences it has against the hazards of life under natural conditions.

The great symbiosis

Jean LOUVEAUX

Flowers, insects: instinctively we tend to associate one with the other, although there is little in common between the plant, which is anchored in the soil and without a nervous system, and the insect with its complex behaviour-patterns. The two are separated by the fundamental cleavage between the vegetable and animal kingdoms. Nevertheless, the flower is unthinkable without the insect and a flower-filled meadow immediately evokes the humming of bees and the flight of many-coloured butterflies. There is more to this image than a commonplace association of ideas; it is, in fact, the expression of a tremendous symbiosis.[1]

In order to understand the full importance of this plant-insect association in the world of living things, let us first consider the plants. We regard apples, cherries or melons as food but to the plant they are simply the carriers for the seeds from which new plants will grow. Each seed, which to us is a pip or stone, carries within its resistant covering a living embryo and its food reserves. This embryo began its development in the centre of the flower, at the moment when two sex cells fused, one from the ovule, the other from a grain of pollen which had landed on the surface of the stigma. Theoretically, one grain of pollen is all that is necessary to pollinate the stigma of a cherry flower, whereas an apple-blossom requires five, and that of the melon several hundred.

The organs which produce pollen, the anthers, are always separated from the central pistil which encloses the ovules. An external agent must therefore be found to transport the grains of pollen, but the journey will be of varying length, and varying degrees of complexity. In poplars for example, or in willows, there is complete and total separation of the sexes, each individual plant being either entirely male and only possessing stamens, or entirely female with pistils alone. This state of affairs is described as dioecious, meaning 'two houses'. Xenogamy[2] is necessary to these plants and an isolated female never bears fruit. Oaks, hazel trees, and chestnuts also have some separation of the sexes, the female and male flowers being present on the same tree but at different points. In the hazel tree, for instance, the male flowers form the familiar greenish catkins which scatter their pollen far and wide from January or February onwards, but it is necessary to look carefully to discover the female flowers, which can be seen only as clumps of red stigmata. Finally, a large number of plants, such as the poppy, have hermaphrodite flowers in which the sexes are joined together side by side.

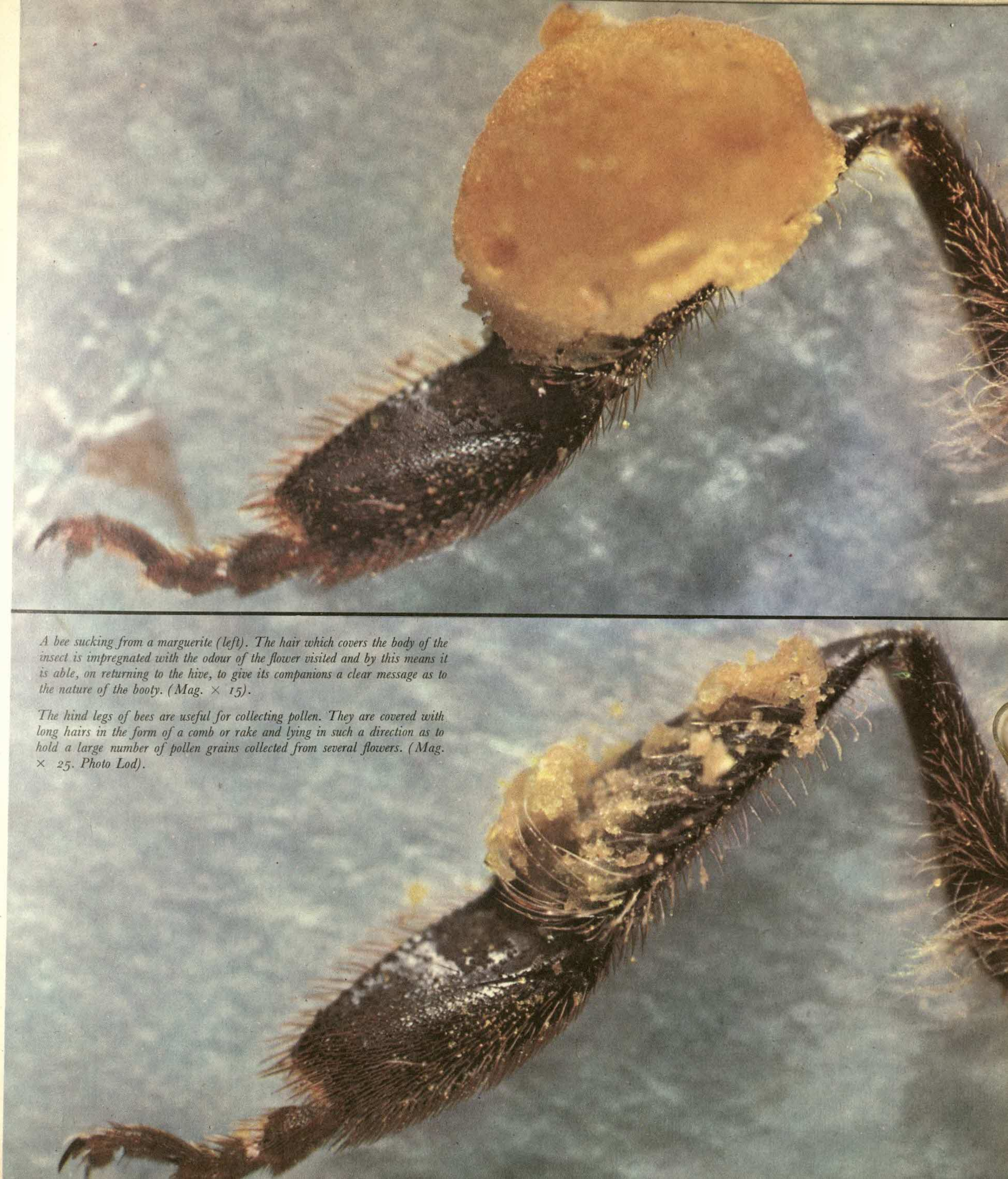
When the sexes in flowers are spatially separated, pollination is usually carried out by the wind and in order to compensate for the relative inefficiency of this method of distributing pollen, the plant generally produces it in large amounts. Thus when the conifers flower in May and June, the falling of their pollen has been described as 'sulphurous rain'.

In plants bearing hermaphrodite flowers, it is ordinarily insects which are responsible for the transport of pollen. They brush against the anthers whilst harvesting pollen, or plunging their tongues into the depths of the corolla in order to suck the nectar[3] cover themselves with the fertilising dust and distribute it over every point of the flower and, in particular, on the stigmata. In these cases autogamy[4] would be the rule if there were nothing to stop it, but in many plants a special arrangement exists in order to prevent self-pollination, with the result that the pollen of one flower cannot fertilise its own ovules.

Separation in space and time

To the separation of the sexes in space, nature sometimes adds separation in time. Thus if the anthers of a flower reach maturity before or after the female organs, this time difference is sufficient to prevent self-fertilisation, and only pollen coming from another flower can fulfil its role. Depending upon whether the sex which reaches maturity first

Butterflies with their long tongues are useful pollinators of the many flowers whose deep corolla conceals the sex organs. (Photo Lod).



A bee sucking from a marguerite (left). The hair which covers the body of the insect is impregnated with the odour of the flower visited and by this means it is able, on returning to the hive, to give its companions a clear message as to the nature of the booty. (Mag. × 15).

The hind legs of bees are useful for collecting pollen. They are covered with long hairs in the form of a comb or rake and lying in such a direction as to hold a large number of pollen grains collected from several flowers. (Mag. × 25. Photo Lod).

is male or female, the flowers are described as protandrous or protogynous.

The primulas have an even more elaborate arrangement to prevent self-fertilisation. If we examine the blossoms of a bunch of the common cowslip, we can see that there are actually two different types of flower, the one with stamens whose stalk is long and pistil short, whilst the other shows the reverse. Under the microscope the pollen of the short stamens is seen to be considerably smaller in size than that of the long stamens, and we know that the pollen of the flowers of one type germinates only on the stigma of flowers of the opposite type. Biochemical studies have shown the presence of special substances in the sex organs whose chemical nature determines the compatibility or incompatibility of pollen and stigma. It seems that this phenomenon must be fairly widespread; for although it is relatively easy to make grains of pollen germinate on a culture-dish of sweetened gelatine, in nature not every grain of pollen will germinate on every style. It may meet a resistance on the part of the other plant which takes the form of a secretion of inhibitory substances and it is interesting to note that, in cases of heterostyly[5] or autosterility,[6] pollen from the same individual is treated as a completely strange pollen.

It would be instructive, if tiresome, to enumerate all the mechanical (e.g., amongst the orchids) or physiological devices employed in nature to avoid self-fertilisation and we may well ask why there exists this preference for cross-fertilisation. Darwin, who, like Sprengel, was fascinated by these phenomena, was the first to show that a multiplicity of crosses between different stocks is of value to the species as a whole and makes it more hardy. Following the example of nature, man began to make cross-fertilisations and the success of these experiments is now well established; the remarkable resistance of hybrid strains of maize is the best proof of this.

We have already seen that the anatomy and habits of insects make them the effective agents of pollination. But it would be quite wrong to suppose that any insect can effect the fertilisation of any flower. In fact, quite the reverse is true, and in some cases, there is only a single insect capable of pollinating a given plant as in the case of an aconite which is only found in regions where the bumble bee capable of fertilising it is also found. More generally, we can distinguish between those plants whose morphology is arranged for fertilisation by the Hymenoptera, such as the bees, by the Lepidoptera (butterflies), or by the Diptera, or two-winged flies. Other large groups play only a minor role in pollination.

Of all insects, the Hymenoptera are undoubtedly the most important for the pollination of entomophilous plants, but even here one must make reservations; for of all the Hymenoptera only the Apoidea bees which represent a small group with only about a thousand species in France, although there are more than 10,000 species of Hymenoptera altogether in the country, have those characteristics which make them good pollinators. Morphologically, they are characterised by having their mouth parts arranged for sucking liquids, by mandibles which are relatively strong and can tear the anthers in order to extract the pollen, by marked hairiness, and by legs which ordinarily bear organs perfectly adapted to the harvesting of pollen.

These hairs, which play an important part in the transport of pollen, are often branched, and this increases their efficiency. Lukoschus has carried out a pollen analysis of the fur of large numbers of worker bees and, according to the plant visited, found an average of from 10,000 to 28,000 grains. One species of bee which habitually visited the flowers of the Indian chestnut was found to carry 51,025 grains of pollen in its hairs, only 800 of which came from plants other than the chestnut, an observation which clearly showed the faithfulness of the bee to the species visited. Other insects, notably the Diptera of about the same size as the bee, carry under the same conditions ten times less pollen than bees.

In the bee, the legs bear organs which act like a brush or comb and sweep the body hairs free of pollen as soon as it is collected, forming it into balls the weight of which may exceed 15 milligrams or about 15% of the total body weight. All the special biological features of the Apoidea help to make them efficient agents for pollination. Their diet consists of pollen and nectar in both the adult and larval states and their life is spent almost exclusively on the flowers from which they gain their sustenance and that of their offspring. The most primitive Apoidea are solitary and, from the evolutionary point of view, not highly-developed, with short tongues, pollen-collecting organs not very specialised, and slow movements. They gather the pollen on a brush, and their efficiency in pollination is less than that of the advanced Apoidea, which include the bumble bee and the honey bee; these, of course, represent the typical pollinating insect, both from the standpoint of their morphology and behaviour and their numbers.

(1) Symbiosis: *a term used to denote the association of two living organisms which are mutually helpful to each other.*

(2) Xenogamy: *a method of fertilisation where the pollen and the ovules arise from different individuals. The term* entomophily *means the transport of pollen by insects;* anemophily, *transport by wind.*

(3) Nectar: *a sugary secretion secreted by specialised organs known as nectaries. These are often located at the base of the flower in the pistil, but Bonnier has shown that they may be found in very varied sites, such as the outside of the flower (extra-floral nectaries). Nectar contains about 25% to 50% sugar (sucrose, glucose, levulose) and 50% to 75% of water. It is very poor in other constituents and therefore does not provide a complete diet, but the combination of nectar with pollen forms a perfectly balanced diet for insects of the group* Apoidea. *The secretion of nectar is subject to a complex rhythm which is related to the hour of the day, the age of the flower, and the environment. From the point of view of plant physiology, it is difficult to assign any precise role to the nectaries unless we are prepared to admit that they exist solely for the purpose of attracting insects for pollination.*

(4) Autogamy: *a method of fertilisation where the pollen and ovules appear on the same flower, and therefore to be distinguished from gitonogamy, a method of fertilisation in which the pollen and the ovules appear on different flowers on the same plant.*

(5) Heterostyly: *plants in which heterostyly exists comprise numerous types which differ in the length of the styles and stamens. Flowers of the same type are unable to fertilise each other.*

In a single year one colony of bees eats more than 40 kg of pollen and about 100 kg of honey,[7] which is produced from about twice this weight of nectar. The number of flowers visited in order to obtain these amounts, runs into tens of millions; a field of rape-seed of about two and a half acres represents about 40 to 50 million flowers producing 40 to 50 kg of pollen and about 70 kg of honey per month, and several good hives are needed in order to make the most of this foodstuff and to ensure normal pollination for the flowers.

How the bee observes the flower

It is impossible to discuss the relationship between insects and flowers without referring to the work of von Frisch, who is best known to the public for his discovery of the bee dance,[8] and has also studied extensively the sight and the sense of smell of bees. It is largely owing to him that we have a fairly detailed knowledge of the visual world of the bee. To us flowers give pleasure because of their striking or delicate colours, but what does this lavishness mean to insects? Do they possess colour vision, or is their universe like a black and white film with nothing but difference in the intensity of the greys to enable them to recognise shapes? Apparently not; for the bee can recognise a blue paper which it has learnt to associate with the presence of syrup and in the same way it recognises yellow and never confuses it with blue. Does this mean that its colour vision is the same as ours? No, for it always ignores red: to the bee, grey and red are just the same, but to make up for this, it can see ultra-violet light which is invisible to us.

On the face of it, it would seem strange that the bee, which is blind to red, visits poppies just as much as yellow flowers, but a spectrographic study of the light reflected by the petals of the poppy has shown that they reflect ultra-violet rays and it is this which makes it possible for the insect to see them. Another peculiarity is that pure white does not appear as such to the bee, since it absorbs ultra-violet rays instead of reflecting them, and white appears as blue-green. So the range of colours seen by the insect is not the same as ours, but nevertheless is such that, far from any confusion with the green of the leaves, entomophilous flowers present a clear contrast to them.

Learning by experience

It remains to be discussed whether the shape of the flowers, the distribution of their colours, and the stripes or dots which seem to indicate the road to follow in order to reach the nectar, have any real value as signposts. Various experiments have provided an answer to these questions, and we know that it is possible to increase the amount of nectar collected by using the same techniques as the plant, that is to say, by indicating the presence of food by such stimuli as sight or smell. Kugler, working with bumble bees, has shown that they prefer to search for food on brightly coloured surfaces rather than on grey ones; they go to the most vivid tones, especially yellow. Discs used to simulate flowers are more often visited when they present a contrast of colours as when the centre is a different colour from the periphery. Radiating coloured stripes have also a very definite power of attraction and a simple triangle of yellow paper with its apex turned towards the opening leading to the drop of sugared water, is enough to guide the bumble bee to its goal with complete precision. Nor is the shape of the disc concealing the sugar unimportant; for a scalloped shape is preferred to a round one.

Lastly, the replacement of the disc by a funnel considerably increases the number of visits, and all these experiments, which it is impossible to summarise briefly, have demonstrated the importance of the role of colour and shape in flowers and the significance of visual landmarks in contributing to their insect-attracting properties. Insects make good use of the coloured signals and signposts in nature to lead them to the nectar hidden in the depths of the corolla and since it is by this means that the flower is fertilised, both are satisfied.

The olfactory sense of bees

Vision, as we have seen, is not the only sense used in the course of collecting honey; for the scent of flowers also plays an important part. Numerous experiments have been devised either to evaluate the respective roles of visual and olfactory factors or to indicate how different parts of flowers vary according to the intensity of their scents. Lex, for example, has shown that the yellow parts of the primrose emit a strong odour, whilst the rest of the plant has none at all. Von Frisch, too has shown that the bee is capable of identifying scents very precisely and using the scent of flowers as a guide to collecting honey. The sense of smell in the bee does not appear to be fundamentally different from our own, although it is certainly more acute. The smell of flowers is easier to learn than odours which are not naturally associated with honey-

Orchids demonstrate some remarkable devices which enable them to pass on their masses of pollen to insects which visit them and thus to give rise to cross-fertilisation.

(6) Autosterility: *autosterile plants have flowers which are identical and hermaphrodite, but the pollen of one plant is incapable of fertilising others of the same plant. This is commonly found in fruit trees in which the varieties are propagated by grafting (asexual reproduction). If the variety is autosterile, autosterility is found in all the trees formed of such grafts. In order to obtain normal fruit production, it is necessary to introduce in the orchard pollen-bearing trees of a different variety.*

bearing plants. The scent of flowers not only helps to guide the bee to the nectar; for on returning to the hive, the one which has found a source of food carries in its hair the smell of the plants it has visited, and this in itself forms a perfectly-understood message for the other honey-bees which enables them to find the source of the nectar or the pollen more easily. This results, of course, in more intense pollination from the point of view of the plants.

We have said a good deal about the Apoidea as transporters of pollen, but if they are the main ones they are certainly not the only ones. Butterflies pollinate numerous flowers which have a very deep corolla, because their tongue is able to unroll to an almost incredible length, varying from three inches to as much as ten in a South American species. Nevertheless, they are on the whole less efficient than the Hymenoptera, since they do not harvest pollen and do not touch the flowers except with their mouth parts.

The Diptera, or two-winged flies, for the most part frequent flowers where the nectar is almost directly exposed to the open, and in autumn one can often see the flowers of the ivy, for instance, covered with flies.[9]

Climax and anticlimax

Sprengel, with his peculiar genius for observation, first noted the remarkable adaptation existing between plants and insects, and later generations have applied themselves to discovering flaws in this symbiosis which do, of course, exist. There is the case of the bumble bee which pierces a hole in the nectar sac in order to avoid the carefully designed mechanism which would make it the ideal pollinator, and another bee which uses the holes made by the bumble bee or habitually steals the nectar of the lucerne flower by slipping its tongue in from the side to avoid contact with the stamen. The baobab appears as if it were suitable for fertilisation by bats, yet its pollen is wind-borne and the pea, constructed as if for insect pollination, is, in fact, self-fertilised. The new generation of biologists does not accept any theory unquestioningly but observes and experiments to discover the true facts. Flowers attract insects and the anatomical and physiological arrangements favouring cross-fertilisation appear to be efficient. The two worlds live in close inter-dependence, but this does not entitle us to ignore the anomalies and complexities that seem to make no sense. Possibly it is a question of vestigial behaviour, or perhaps there has been a superimposition of several solutions to the same problem, the one complex and random, the other simple and efficient. Maybe we are even observing a stage of evolution, and entomophily, with its marvels of adaptation and refinement, might once more be replaced by wind pollination as in the Graminaceae or grasses.

HISTORICAL NOTES

1682
NEHEMIAH GREW employing the microscope, which had just been invented, produced the first description of grains of pollen.

1793
KONRAD SPRENGEL published his treatise entitled Das entdeckte Geheimnis der Natur im Bau und in der Befruchtung der Blumen *(the Discovery of the Secret of Nature in the Construction and Fertilisation of Flowers). This publication was totally misunderstood by his contemporaries, and he died twenty-three years later virtually unknown. In 1943, Karl von Frisch, said of this book: 'Many doubts and criticisms have been directed against it but they have all been demolished and, like a rock, his teaching still stands.'*

1860–1882
DARWIN'S experiments on flowers in which he showed the importance of cross-fertilisation.

1878
GASTON BONNIER submitted his thesis on nectaries.

1898–1905
Publication by KNUTH of his great biological treatise on flora.

1920 *to the present day*
The work of KARL VON FRISCH and his pupils on the sensory physiology of the bee, its colour vision, perception of smells, etc. Discovery of the 'dances' which provide communication between worker bees.

---

(7) Honey: *the figures may give a false impression of the harvest actually produced in a hive. The amount removed by the bee-keeper (10 kg per colony per year) is only a fraction of that collected by the bees.*

(8) Dances: *see the chapter on 'The Language of Bees' by M. Lindauer.*

(9) *It is, of course, not only insects which pollinate flowers. Thus birds and bats act as pollinating agents of numerous tropical plants.*

PART FOUR

Animals and men

Wood ants (Mag. × 5) (Photo Lod).

The intensive breeding of ants

Karl GÖSSWALD

The red wood-ant is one of our useful allies against insect pests, and in a suitable environment a nest of ants is able to kill and store more than 100,000 of these pests in a single day. Wood-ants also play an important role in improving the soil and in transporting seeds, yet in many areas their nests have been destroyed and the ants have almost disappeared.

Today, because of their usefulness in forests, wood-ants are protected by law and have been so for the past fifteen years; the destruction of a nest of ants can cost a German as much as fourteen days' imprisonment or 150 German marks. But it is not sufficient simply to protect the existing colonies like rare plants and animals. If our woodlands are to be improved and protected from insect attack, ant colonies must be actively introduced wherever the number is less than about two per acre.

Not every species of ant is equally effective in protecting the forests. For example, the large red ant (*Formica rufa rufa* L.) is one of the less efficient species since its colonies are relatively small and survive only a brief period. This is because there is only one queen, whose odour spreads uniformly throughout the nest, with the result that the ants are not very sociable and colonies with only a single queen are unable to separate in order to form new colonies. Instead, new colonies of large red ants are built up in a strange way with the help of another species (*Serviformica fusca* L.). The young queen of the large red ant introduces herself to the *fusca* workers and makes them raise her young ones, after having already killed their own queen; thus after the death of the *fusca* workers, the colony, at first mixed, becomes purely and solely composed of *Formica rufa*. When the *rufa* queen dies (often at the age of twenty years) the colony becomes extinct; all these biological features are extremely undesirable and the colony of *rufa* is almost useless for the protection of forests.

It is therefore much better to use other smaller forms of wood-ants which have colonies provided with numerous queens, sometimes as many as 5,000 in one nest, and for this purpose the *Formica polyctena* of the flat zones or hilly regions of central Europe is particularly suitable. Further north, or in the mountainous area of central and southern Europe, one can also find *Formica lugubris* and *aquilonia*, which are suitable for the artificial establishment of colonies. These ants with many queens have certain important characteristics: each nest contains 500,000 to three million individuals. Different nests, although of the same species, group together into 'federations', and such 'federations' sometimes comprise several hundred nests. The additional advantages of these species are that a colony can be rejuvenated by the rearing or adoption of young queens, and that the number of nests can be increased by division into daughter colonies.

The biological peculiarities of ants enable them to give uninterrupted protection to forests. The temperature-control arrangements in the nest make it possible for them to survive the worst weather, whilst the activity maintained during the whole period of vegetation makes the ants independent of the stages of development of noxious insects. The social organisation of colonies enables the normal rivalry between individuals to be replaced by a common purpose and, to obtain some minor independence from their insect food supply, the ants harvest the honey-like substance produced by the tree-aphis. These insects are not harmful to the forest and provide a convenient alternative food supply when others are scarce.

In densely populated colonies a mechanism exists which is effective against epidemics and under- or over-population. It takes the

Wood-ants attacking a caterpillar. (Drawing published by the permission of Pr. Mario Pavan, Italian Minister of Agriculture and Forests).

Opposite page

Life in an ants' nest: a worker carrying a pupa. (Mag. × 25. Photo Lod).

form of regulating the proportion of the sexes, so that more females are produced in large nests in sunny situations, and more males in the less densely populated nests situated in the shade. There are other less important differences in the ecological and biological peculiarities of the various sub-families of wood-ants, some of which are not structural but biochemical and can only be discerned by paper chromatography (a kind of chemical analysis). Yet although the differences may be small they can be important when trying to build up the ant population in a given area, and so it is usually worthwhile to discover exactly what they are.

Protection of red ants

Nature conservancy regulations, conferences in schools, information given in the press and on radio are of great importance in ensuring that people understand the need for ants[1] in forests. But in addition it is necessary to supervise forests and to protect the nests against their natural enemies such as green woodpeckers,[2] and badgers, as well as humans.

A very efficient form of protection is to cover the nest with a wire grill; for preference, conical shaped wire netting (of mesh 1–2 cm diameter) is employed. It is to be hoped that the creation of ant farms will eliminate the necessity for implanting fresh nests and thus reduce the cost, already high, of this method of protecting forests. By using artificial processes it is possible to set up daughter colonies containing an average of about two hundred queens. We can only find these queens during a brief period of about a fortnight in spring, when the days become warmer; for later they bury themselves deep in the soil. The ants which awake from their winter rest assemble in a dense mass at the surface of the nest and warm themselves in the sun and it is unnecessary to take all the queens from the same nest to set up a new colony. The nest need not be divided into two equal parts; we simply remove from the productive nests (unless these are of an exceptional size), 10 to 20 gallons of ants from the central most densely inhabited region. They are soon replaced by ants living in the neighbourhood for a nest contains 40 gallons of ants (100,000 to 300,000 workers), and the hole is filled up with twigs and other material from the nest.

The container holding the ants is tightly stoppered, with small holes for ventilation and appropriately marked. When the containers are filled a note is made of their origin and the approximate number of queens, which are distinguishable by reason of their size and the brilliance of the posterior part of their abdomen. It is necessary to keep the containers in the shade, out of bright sunlight and in order to make a new colony the contents of four such containers are mingled so that the queens are equally distributed. The new colony can be placed in pine, fir, oak or larch woods, or better still, in a wood of mixed trees. A tree-stump forms the centre of the nest and the ants prefer a site where there is plenty of sunshine, such as the edge of the wood or in a clearing.

For a start twigs are placed on the stump and then the ants from the containers followed by more twigs and more ants. The whole is then covered by a netting which gives the necessary protection in the early days. During the first weeks it is particularly important to inspect the colony which may have moved from its original site and requires to be protected anew. In employing this method over a period of thirty years we have established more than 5,000 nests in ninety different biotopes,[3] which has made it possible to discover which colonies can be most successfully divided up. Then, by selecting queens from these colonies, we develop those breeds of ant most suited to our purpose.

The raising of queens

Out of the thousands of young males and females that swarm from the ants' nest in spring, only a certain number, after mating, are accepted into a colony of their own species. In our researches the ants were automatically caught at the moment of swarming and taken to the laboratory for fertilisation, following which the impregnated females were introduced into new colonies as young queens.

The artificial rearing of queens has had four results which have proved to be extremely important in the raising of ants:

1. The artificial queens can be used to reinforce a colony which lacks sufficient queens of its own and the colony reinforced in this way can be divided up more frequently in order to produce daughter colonies.

2. New colonies more rapidly reach the size at which they can be divided because the rate at which they grow increases with the number of laying queens.

3. The prolongation of the growth-period of a colony is from three to five months. This is valuable because during the rather short period normally available for splitting colonies foresters are often busy with other jobs.

---

(1) *Ants are also used directly by man. Their eggs and larvae are used as food for fish, song birds, pheasants, etc. and formic acid is used in the treatment of influenza, rheumatism, and other diseases.*

(2) *A woodpecker can, throughout the year, destroy several hundred wood-ants a day, and woodpeckers are particularly destructive to artificial nests.*

4. Queens can be selected from a known and suitable stock, so that the new colony can be set up in a place which lacks its own nests with some certainty that the ants will be of a type that can survive in the new surroundings.

In order to carry out this artificial rearing it is necessary to use healthy nests which have shown themselves to be capable of reproducing freely, and to be able to distinguish between males and females and establish their periods of swarming. The males are entirely black, and recognisable by their sexual organs, the females have a brownish-red head and back and the tip of their abdomen is cone-shaped. At the start of the swarming season one finds mainly males and at the end mainly females, the latter predominating in fir woods which are not too thick and, in spring, in larch woods which at that time are sunny because the leaves have not yet appeared. It is possible to change nests containing predominantly female ants into nests containing predominantly males by covering them from January until the early stage of the development of the larvae with green branches of fir and larch, and the reverse is the case if predominantly male nests are left uncovered and exposed to light. For at temperatures below 19°C the queens lay unfertilised eggs from which males emerge, whilst at higher temperatures the eggs are fertilised and produce females. The difference between the queens and workers coming from eggs hatched later in the year, can be seen at an early stage and when the queen larvae emerge they are given special food, a secretion from the salivary glands, whilst the larvae of the workers receive only regurgitated food.

The winged ants (both male and female) usually seek a projection from which they can take to flight and it is at this moment that they can be trapped in an appliance surrounding the nest. A suitable method has been devised which prevents them from escaping and enables them to pass through a tube into a bottle within which, in good weather, many thousands may collect. The plastic bottle we have used contains a substance designed to maintain the high humidity which ants require and to prevent the accumulation of excessive amounts of the formic acid secreted by the insects. Small holes assure adequate aeration and the bottle must be kept from the direct rays of the sun.

In order to bring about a population increase, approximately equal numbers of males and females are placed at 25°C in glass containers over humid soil and workers which have been captured at the same time feed them with honey that is either provided for them, or the males and females can feed themselves. Mating is encouraged by radiation from an infra-red lamp, and after this the queens lose their wings and the males die.

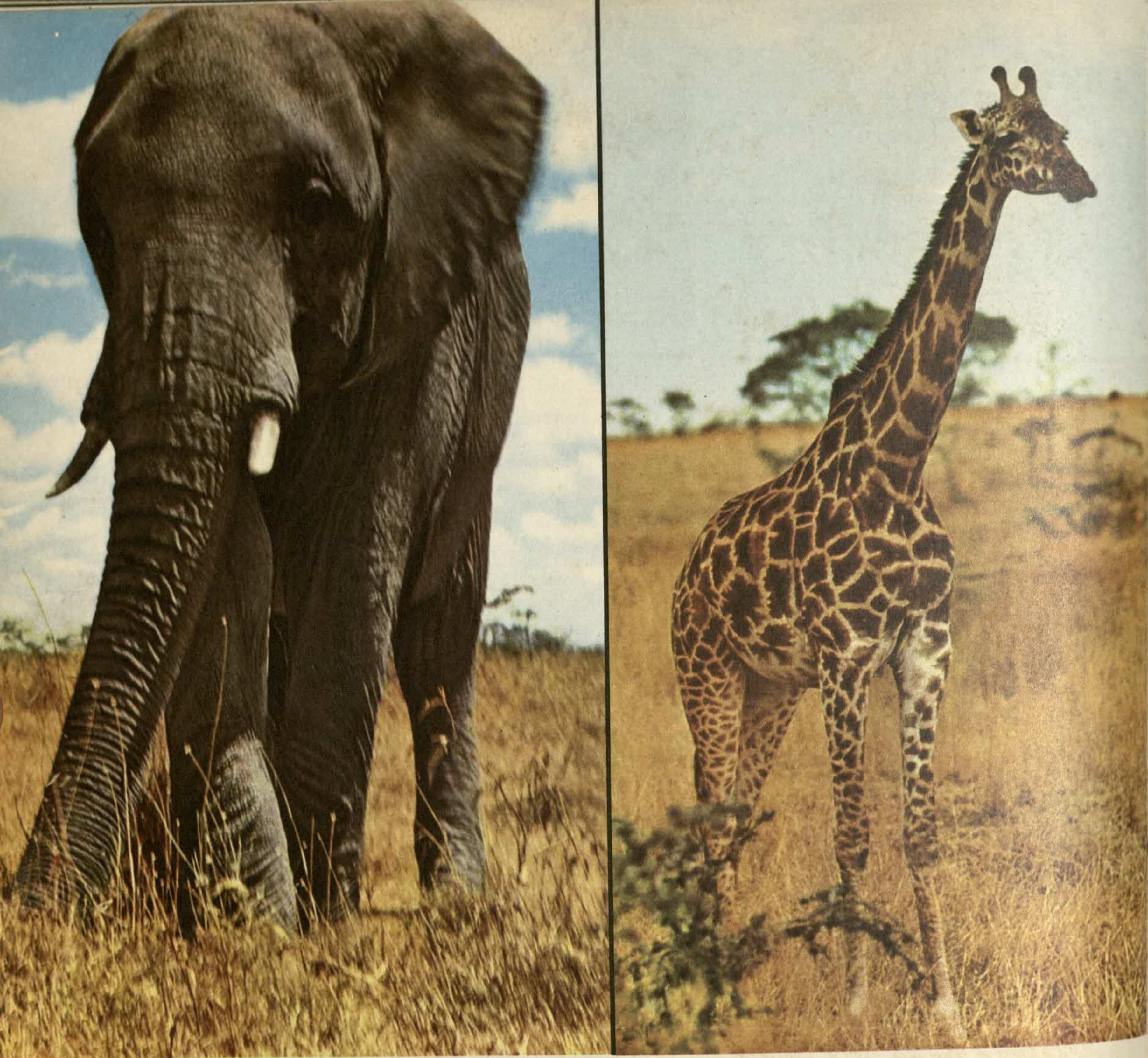
An interesting method is employed to separate those queens which still have their wings from those which have already lost them, since we know that the former will move towards light, whereas the wingless ones move away from it and congregate in a darkened tub. After they have segregated themselves in this way, the fertile queens are removed by an electrically-driven suction pump and placed in a glass container, each group of a hundred queens being enclosed in a special tube ready to be sent out for introduction into another colony. The tubes are then grouped in batches of fifty, and more than one and a half million queens have already been sent out in this way.

It is best to introduce queens into a colony as soon as it is set up, but sometimes it is first necessary to accustom the colony to the odour of the new queens. This is done by using a special tube, one end of which is pierced with small holes and the other end open but with a drop of paraffin oil on its lip to prevent worker ants from crawling out; about two hundred queens and four hundred workers are put into the tube together with some honey and the tube is buried near the nest. The following day the number of workers is doubled and after four or five days the workers will have become accustomed to the queens and can then be introduced into a hole a foot deep in the dome of the nest. When this is done losses are small and there are only occasional attacks on the queens by the workers, following which acceptance takes place. We know, too, that during cold weather, early in the morning or late at night, the worker ants are less likely to attack than during the hotter hours of the day.

In the ants' nest the workers devote most of their time to the care and upbringing of the pupae. They are shown here carrying eggs.

---

(3) *Biotope: see note 3, p. 154.*



From the beginning, man has maintained a more or less direct relationship with the animal world. We have seen that biologists in their experiments ordinarily make use of animals such as insects, birds and small mammals, but this is only one aspect of a vast symbiosis which ranges from the hostile relationship between the hunter and his prey to the training and domestication of more familiar animals. The list of animals capable of being trained is extraordinarily wide, including the whale and elephant at one end and the fleas of the old fairs at the other, and in passing it includes the ostrich, the tiger and the snake. Some stately animals such as this giraffe and the elephant, finally submit to the wishes of man and the pages which follow show how he has been able to impose his will upon them. (Photo Picou).

The training of animals

Bernard RICHARD

The milkman's horse is trained to stop at the door of each customer, a poodle in a music hall is trained to push a pram, white rats are trained to run a maze or to press a lever to obtain food, the sea-lions at the zoo are trained to catch fish in the air for the pleasure of the spectators, and even the tiger can be trained to walk on a wooden ball. . . .

One could make a long list of those animals which are capable of being trained: it would range from the elephant and the whale (since the building of the large sea-aquarium in Florida where zoologists devote themselves to studying these large aquatic mammals), to the performing fleas in the fairs of our childhood.

The training of animals has a variety of aims in view:

(*a*) The stopping of the milkman's horse and the catching of food by sea-lions has developed fortuitously or else with a practical aim in view.

(*b*) On the other hand, animals used in the laboratory are deliberately trained with a scientific end in view. It is, in fact, the first step to be overcome before beginning the experiment proper. Only after the animal has become familiar with the apparatus can variations in its behaviour be interpreted as a response to environmental variations introduced by the experimenter. Thus when a white rat has learned to push a lever to receive food under ordinary conditions we can then proceed to observe the effects of an injection of caffeine. The training has the sole purpose of getting the animal to get to know the maze as a means of carrying out an experiment.

(*c*) The aim of training in a circus is neither practical, fortuitous nor scientific but aesthetic, being carried out in order to achieve some apparently remarkable result with large or dangerous animals for the pleasure or awe of the spectators. Here the training is not the means but an end in itself. However, as we shall see, the science of behaviour has much to learn from the circus and to ignore it is to lose a novel aspect of animal psychology.

The apprenticeship

The training of laboratory animals—the apprenticeship—rests on a hypothesis: that it is possible to know the behaviour of an animal in the pure state[1].

If this be the case, the experimenter must withdraw himself as far as possible in order to eliminate any emotional factors existing between himself and the animal: at the end of the experiment the animal ought to be in the same emotional state towards him as at the beginning. Thus he will choose for preference domestic animals or those completely tamed.

Clearly, Pavlov's postulate was vulnerable, as was his belief that he could gain knowledge of the animal world based wholly upon animals made degenerate by artificial selection. More and more the experimenter prefers to leave the laboratory and go back to nature where he will find a more genuine creature which he can approach with the same objectivity as in the laboratory.

Completely different from the above is the training practised in the case of wild beasts, which follows a method diametrically opposed to the preceding one. The animal is wild and mans' task is to impose himself on it to the point of submission. Or, even better, the trainer should aim at a degree of acceptance which allows him to be adopted by his pupils as one of themselves. He animalises himself by a sort of zoocentrism.

Anthropocentrism tends to an assimilation in the opposite direction: man lends, as it were, his own psychology to the animal. This approach has always vitiated our knowledge of animals by reducing them to carrying out edifying but nevertheless puerile performances. Recently, however, psychologists have used it with greater objectivity as when the Kellog and then the Hayes family, adopted young chimpanzees and reared them together with their own children of equivalent ages.

Of course, no such thing occurs in circus training. The animal has no chance to be admitted into the society of men, it is man who

Despite his ferocious appearance, the lion is one of the wild animals which can be trained most easily and with the greatest success. (Photo Picou).

---

(1) *The Russian scientist, Pavlov, was one of the greatest supporters of this idea which is less generally accepted today, and even believed he had put it into practice by placing dogs under severe conditions of isolation. By such methods he satisfied himself that he had cut all the ties which necessarily unite the experimental animal with the experimenter and had thus banished the sources of anthropocentric error.*

(2) *See above the chapter entitled 'Social Hierarchies'.*

imposes himself upon them as one of them, using constraint when necessary, but preferably his superior intelligence. Thus, the training completed, the initial relationship between the man and the animal has completely changed and a new equilibrium is established.

The psychology of constraint

No longer do we have small and gloomy cages within which the wretched captives die slowly for the entertainment of visitors. We now possess a wide knowledge of how to breed and keep alive wild animals in captivity and sentimental well-wishers are wrong in misplacing their sympathy when they plead for the 'liberty' of the kept animals. Life in the zoo permits many species to live comfortably without fear from enemies, to reproduce, and to reach an age rare in the natural state.

In the natural state, in fact, one never finds this golden freedom which so many believe to exist. The restraints under natural conditions are ever-present, even for the strongest: they are known as 'territory', 'dominance' and 'fleeing distance'.[2]

Territory

In the circus, as in the zoo, the territory of each animal is often considerably reduced because of limited space; but the inconvenience resulting from this is partially compensated for by man. Territory being related above all to the necessity of feeding, the problems caused by this are greatly diminished when man supplies the provender regularly.

Within the limited circumference of the circus ring different species enter into relationships which would never occur in nature. In particular, similar species (lions and tigers, for example) have little chance of meeting each other under natural conditions for the obvious reason that they inhabit different continents: the lion is African, like the panther, the tiger is Indian, whereas the jaguar and the puma are American. The forced meeting of these animals brings into being a new type of territory: struggles and associations take place between them without reference to their specific differences.

For each individual the cage in which it is transported takes on the significance of the principal territory, whereas a given part of the training cage (the stool, for example) is a territory of the second order. The animal never requires to be entreated to return to its cage and its stool becomes for it, with the complicity of the trainer, a place of relative calm and repose.

Fleeing distance

The hunter knows that one is not able to approach all animals with the same facility. Certain birds, such as the magpie, seem to take a malign pleasure in allowing one to come as near as possible before flying away just on the point of danger; others seem completely lacking in distrust, such as the male chaffinch in the spring or the robin in winter, which will come and eat out of one's hands. One is liable to suppose that these animals understand our intentions towards them but, in reality, each species is characterised by a minimum distance beyond which a dangerous being is unable to approach without causing flight. This is what is known as the 'fleeing distance'.

On the other hand, if the situation arises that an animal is unable to flee but remains cornered, it will put up a defence against its aggressor when a certain distance, equally characteristic, is reached which is known as the 'critical distance'.

In captivity, particularly in the circus, the fleeing distance and critical distance can become very much reduced and even abolished among tamed animals. If they persist—as is the case during the beginning of training and in old animals, high in the hierarchy—the trainer possesses a natural means of making them move without touching them. On passing the fleeing distance he makes the animal retreat; in continuing to the critical distance he makes it turn towards him; a simple method, but dangerous, because it is necessary to know how to stop an animal from attacking.

Dominance

We have seen in another chapter[2] that interspecific dominance is possible because of the 'tendency to assimilation' by which an individual of one species, accustomed to being alongside another, ends up by forgetting the biological barriers which separate them and no longer considers itself as a stranger but as a companion or a rival. Man can in this way be admitted to the society of animals and it is hardly necessary to point out that in such cases he will be the 'alpha' individual. He must not only occupy the territory by arriving first but by walking in a provocative manner. It is his duty to nip in the bud all attempts at rebellion, to protect the weak against the strong, and, in short, play the pre-eminent role.

It may seem strange that man is capable of taking part in an animal society, but without

To train certain very wild species, such as zebras, man has to bring into play all his knowledge and experience of animal behaviour. (Photo Picou).

(3) *Dogs and horses which seem to calculate for a long time defeated the understanding of experts. But by now we realise (Buytendjik) their ability comes directly from their trainer's cues even without his being aware of it.*

(4) *The name given to each animal in itself serves this purpose because it attracts the attention of a particular animal and directs orders to the right destination; it soon suffices to shout this name.*

(5) *In his memoirs the trainer Court recounts how he penetrated for the first time into a lion's cage without any preparation except attentive observation of the last training by his predecessor. With the help of a boy, he was able to remember several of the necessary key gestures. The sequence of movements was fortunately very simple: four lions (of which one named Nero was fierce) were to be seated on their stools. After that, they were to be assembled on a pyramid before returning to their stools once more. Hidden behind the pyramid, Court awaited the arrival of the three friendly lions. They entered*

Continued on next page

bringing in the problem of those cases where human children have been actually adopted by animals it is by no means a figure of speech to say that we are fundamentally a part of nature. It is only our anthropomorphism and our great ignorance of the world of wild animals that leads us to believe that our own species ought to be considered by the animals as radically different from all others.

We must now consider how the trainer, having acquired the right to be in his group of animals, begins to teach his pupils. How does he bring them to follow his instructions?

Training procedure

The very great variety of animals susceptible to being trained corresponds to an immense scale of psychologies. The tiger is powerful, fierce, uncertain; the polar bear enigmatic because nothing in his attitude transmits his emotional state and the tamer has great difficult in knowing what passes behind its mean-looking little eyes; the jaguar appears obtuse, awkward and as stubborn as ten mules; the elephant docile and wise; the sea-lion playful . . .

In any given species there is an even greater variation in character: certain panthers are easy, gentle, confident, and others as dangerous as tigers. The same animal changes character with age. Young and still wild, it will attack man as an inveterate enemy; adult and well trained, it comes to accept him as a companion and someone to be protected from individuals of its own species; advanced in years, it sees in him a rival for the conquest of dominance which makes it jealous and watchful for the moment when it can supplant him.

All animals possess to an exceptional degree the ability to perceive the emotional state of their neighbours, whether man or beast. Deprived of a conscious language they are able to grasp from imperceptible signs the slightest variations in the feelings of others. It is commonly said that the dog knows whether its master leaves the room to go to another or in order to go for a walk; it also knows when its master is ill; it goes towards him when it seems to us that it is still beyond reach of his senses. Not possessing the exquisitely delicate receptors of animals, we believe this to be a miracle when it is merely the ability to differentiate, in a highly refined manner, gesture, scents and the passage of time.[3]

Consequently, if the trainer patiently develops his powers of observation so as to perceive the subtle changes of mood in his pupils, he is assured of being at each instant perfectly in accord with them. But should he lose confidence in his superiority and begin to fear them he is lost; the vicious horse will throw him or the lion seize the opportunity to attack him. Even so, it is possible to institute some sort of language between man and his animals. The trainer employs firstly nuances in his voice, so that the inflexions of anger, authority, or gentleness come to be perfectly understood. It is possible to make use also of what nature offers him for each species; but this method demands a certain talent. During periods of training the tamer Court used to calm and recompense his tigers with a certain 'Prrr', imitating these animals when they are satisfied: the same idea is expressed by the 'Ooo, ah, ah' for lions. This innate language is useful because it allows an animal to understand immediately when its master is pleased; but it has the disadvantage of being limited and to express not a specific order but an emotional state. Thus in addition to the above the trainer has to create an artificial language which is more general and persuasive.[4]

It is other signs, however, peculiar to each trainer, which have become by association and repetition a sort of code. These are very often so slight and imperceptible to the spectator as to pass unnoticed because they are the result of a progressive symbolisation of gestures which have their origin in material effectiveness. The lashing of a whip destined to hit a non-docile beast is reduced to an imperceptible movement of the hand or even to the intonation of the voice which has always accompanied this act. To tame four particularly vicious old lions, Court used a blunted pitchfork from the end of which jingled a box of bells. The original brutal shock of this pitch-

The training of wild horses, which is part of every rodeo in America, calls for the solid qualities of vigour and endurance. (Photo Holmes-Lebel).

Continued from previous page

without seeming to take any particular notice of him and started to play. An order, punctuated by a crack of the whip and the three lions went to their stools. Encouraged, Court made Nero enter the cage and he, too, obeyed. A fresh crack of the whip and Nero climbed down walking towards Court, who, frightened, prepared to beat him; but the animal, in great style, passed him by and leapt to the top of the pyramid as he was intended to do at a signal from the whip. Without any order he had started his work. The three other lions did the same; then at the given order they returned to their stools. Nero, however, refused to obey: repeated cracks of the whip, shouts in turn appealing or authoritative, could not make him leave his perch. The key-gesture was missing. Court came out in a cold sweat, but very fortunately the boy remembered that it was necessary to stroke the lion with the whip on passing behind him. In spite of several cracking blows a few inches from his skin, he did not move. Finally he was touched and with one leap bounded onto his stool. He had only been waiting for that single gesture.

Training of police dogs: at a signal, the dog which until that moment had stood stock-still, leaps onto the thief.

fork in the flank of the animals remained forever related to the noise of the bells which sufficed thereafter to suppress their exuberance. The same principle applies to the strap used for raising and holding the hooves of young horses for changing their shoes which can be replaced later by a gentle tap. This communication between man and animals does not merit the name of language any more than the sounds emitted by most animals, because the sign is not separable from the particular thing signified and has no universal value. It is primarily a means of showing one's feelings, because, ultimately, the trainer has nothing to communicate to his pupils other than his pleasure or displeasure: satisfaction when he is obeyed and dissatisfaction when he is not. It is up to him to know what he wants of them and to create the habit in his pupils.

It is not unknown for much deeper ties of friendship to develop between trainer and animals. It is in general the 'omega' individual, the gentle sufferer of the group, which is destined for this role. More docile, indeed even affectionate towards man, it is his lot to carry out the most difficult manoeuvres because he learns more quickly and is not opposed to training. The difficulty of training does not come solely from the material difficulty which the animal might have in accomplishing the movement but from other obstacles and above all from its passive resistance. If they are obstinate and blessed with great strength the task is not easy. It is necessary to employ patience but also force and even mechanical methods as when, for example, one is making an elephant perform an unnatural movement.

The attraction of a reward can be an effective weapon in the hands of the trainer. To have a piece of sugar a dog will willingly yield to the wishes of his master. With five vicious tigers Court used this method with success: initially, so that they understood that the training cage and the trainer had a positive value, no food was given to them outside the cage. He was then able to get them used to new and often disquieting situations.

The trainer very often makes use of these psychological mechanisms, which we have named territory, dominance, fleeing distance and critical distance. Should he wish to teach a novice tiger to climb onto a stool, the trainer draws near to it and provokes it into an attack against him. The whip enables him not to provoke the attack from too close; when the tiger is lured into the attack it suddenly finds the stool in its path and has little choice but to jump onto it. At this moment the whip is withdrawn thus removing the cause for the attack and the voice of the trainer expresses his satisfaction. The tiger quickly learns that the sitting position on the stool is an occasion for reward and a place of relative tranquillity. The whole movement is repeated until the animal knows the sequence of gestures: provocation, flight, critical reaction, installation on the seat, reward and relaxation.

Chance is frequently important and the trainer will often exploit a tendency which has developed of itself: a lioness reared up one day when provoked by the whip and Court exploited this aggressiveness into a fixed ritual of sitting up and begging.

Inertia is not the only obstacle which the trainer has to overcome. It is necessary to teach the animals to become accustomed to the movement and noise which are part of circus life, or to neighbouring, unfamiliar species which might be either rivals or potential prey.

When the trainer has obtained obedience and a certain understanding of the movements to be accomplished it only remains to multiply the exercises to obtain a sequence of associations. Thus the movements automatically become linked together and it only requires a few small signs on his part to lead the beasts through the whole act.[5]

A type of pedagogy

So the tamer practises psychology without always realising it. His first efforts are to become accepted in the animal society. He will extract great advantage from this: admitted as the leader he will benefit from the laws which reign in this society. He is no longer the stranger and enemy to whom one submits by force but the companion whose caresses are appreciated and who is protected as a friend against the jealousy or rivalry of others.

But this situation imposes upon him certain obligations. He must defend the weakest, who will sometimes even seek refuge behind his body. His pre-eminence must be preserved by an incessant moral struggle because dominance is not, happily for him, a matter of physical strength. The slightest relaxation or poor physical health resulting in a lowering of confidence, may be his undoing and leave him at the mercy of the animals. Thus he must be continuously on guard in order to detect the slightest change in mood and forestall a revolt.

Ultimately all this is not very different from education and we can say without paradox that one leads a group of lions and tigers just as one leads the fifth form at school.

The laboratory animal

Michel SABOURDY

Experiments on animals and the experimental method in biology have evolved along parallel lines throughout the centuries. One has merely to survey the history of biological science and medicine to find that at the heart of each great discovery there lies an animal. The way in which the animal is used and the aim sought vary and evolve, but in most cases the animal is there as a substitute for man.

Over a long period of time, between classical antiquity and the nineteenth century, animals were used in order to acquire knowledge of man's anatomy and physiology. The animal was regarded as a passive model which could be observed and dissected in order to understand its structure and mechanism, so that this knowledge might be applied to the human organism.

With the advent of microbiology towards the end of the nineteenth century, and the development of immunology, the discovery of hormones, vitamins, and the growth of modern therapeutics, the idea of the laboratory animal, as it exists today, was born.

The animal is now not only a model but basically an organism which can be studied for its reactions to various treatments: the inoculation of germs, the injection of chemical or biological substances, and physical responses; it becomes a biological reagent similar to those used by the chemists. The ideal laboratory animal is now an organism which is perfectly understood, with normal, constant, reproducible reactions, which enable the biologist on the one hand to attribute the results of his experiment solely to the method employed and on the other to compare these results with earlier or contemporary ones.

Until the beginning of the twentieth century, animals used in research did not form a very specialised category. It was the period of the 'white rat' or the 'white mouse'. Such creatures were adequate at the time because the experimental results were ordinarily qualitative. Today biological research is essentially quantitative, as when we measure the variations in the weight of an organ, or the percentages of various biological substances in the body. Moreover, many products of biological origin, such as certain hormones and vitamins, are measured in animal units. Therefore it is essential to work on homogeneous animal material which reacts in a constant manner.

The range of organisms

The greatly varying kinds of research require as varied a range of organisms as possible. The species of animals known as 'laboratory animals', such as rats, mice,

(1) *'The introduction into laboratories of a new species having the same general qualities as known experimental species, if it does not merely duplicate these, is a valuable advance.' (Charles Nicolle).*

(2) Breed: *a group of organisms with known ancestors. A breed generally presents some characteristics which differentiate it from all others.*

(3) *The C3H breed of mice can be given as an example:* 94% *of the females have breast tumours at about nine months.*

(4) Inbreeding: *the mating of two organisms having some degree of relationship, that is, having ancestors in common.*

(5) Homozygosis: *a state wherein two corresponding loci in a pair of chromosomes are occupied by identical genes; an organism can be homozygous for one or more genes or for all its genotype. (See Vol. I of this work: 'Problems of Heredity'.)*

(6) Inbred stock: *a breed which has been kept alive by the mating of brother and sister for at least twenty consecutive generations.*

(7) *Percentage of heterozygosis remaining after several generations of brother-sister mating (S. Wright, 1921). The figures in light print represent the generation examined; the figures in heavy print the percentage of genes in a heterozygous state:—* 0: **50.0**—1: **37.5**—3: **25.0**—5: **16.4**—7: **10.7**—9: **7.0**—15: **2.0**—20: **0.7.** *After twenty generations of reproduction between brother and sister, theoretically 99.3% of the genes of an organism are homozygous.*

Guinea-pig, of stock F, with reddish fur, pigmented skin, and very prolific.

guinea-pigs and rabbits, has today been greatly extended; biologists[1] now use more than fifty different kinds of animals and with the development of research the list grows ever larger.

The needs of research have brought about in some species (rats, mice) the creation of many breeds having specific characteristics:[2] sensitivity to gonadotropic hormones, to radiation, experimental tuberculosis, neurotropic viruses, appearance of leukaemia at a given age or spontaneous tumours in a constant location. These breeds are reared from individuals which have developed spontaneously some biological characteristic such as extreme sensibility or resistance to chemical, physical or other agents.[3] The combined action of selection and in-breeding makes it possible to stabilise those characteristics which will be specific to the breed thus created.

In-breeding[4] is in fact the only way of obtaining homozygous organisms,[5] that is to say, we eliminate from an animal population variations of genetic origin and thus obtain, theoretically, a group of individuals with identical and constant known reactions during succeeding generations. The term 'pure breed' frequently used to indicate an inbred stock[6] of laborarory animals is however incorrect, since it is doubtful whether one could obtain in higher organisms individuals homozygous for all their genes, as might be expected from the theoretical laws of genetics.[7] It is more probable that some residual heterozygosis[8] continues even in breeds which have been closely inbred for dozens or hundreds of generations. This heterozygosis and the appearance of spontaneous mutations maintain within the inbred stock a genetic variability which explains the discrepancies found in some experimental results obtained from inbred animals.

Heredity and environment

The phenotypical characteristics[9] of an organism which interest us in laboratory animals, are not only hereditary but are the result of an interaction between heredity and environment and therefore, together with genetic stabilisation, it is essential to exert a strict control over the environment in which they develop, in order to obtain uniform stocks of animals. Environment in its widest sense includes food, temperature, humidity, light, noise, the staff looking after the animals, in short, everything which forms the atmosphere of the breeding chamber.

Laboratory animals, in order to fulfil their rôle of trustworthy reagents, must also be healthy, that is, they must not only show no signs of clinical disease, but must carry no latent infection; for germs can be present in apparently healthy animals. This animal/germ association makes the laboratory animal a biological complex which can only persist under specific conditions and this balance can easily be broken if these conditions are altered in equilibrium as during a change of environment or in the course of an experiment. This can result in the animal's death from infection or the activation of germs in a latent state. In both cases, the work of the experimenter is made more complicated or even rendered useless.

Aseptic animals

Techniques have been developed (Reyniers, 1953) which make it possible to produce aseptic animals.[10] These methods are based on the fact that before birth the young are protected from all infection and the animals, if removed by caesarean section and kept in a sterile cage, are aseptic, that is to say, free from all germs.[11] The possibility of producing aseptic animals which extends to the higher organisms the concept of pure culture, is therefore a means of knowing more precisely their behaviour vis-à-vis various stimuli from the outside world. These animals form the ideal instrument for the study of such important questions as the origin of antibodies, the pathogenic power of various germs, the virus aetiology of cancer, metabolic diseases,

(8) Heterozygosis: *State in which two corresponding loci are occupied by different genes.*

(9) Genotype and phenotype: *all the hereditary factors, whether apparent or latent, are referred to under the name of the genotype. All the characters, hereditary or otherwise, which can be seen externally, are called the phenotype. Individuals presenting the same external characteristics are phenotypically similar but can be genotypically different.*

(10) *'Without wishing to make any positive assertions, I cannot conceal the fact, that I would undertake this study [on aseptic animals] if I had the time, with the preconceived idea that life under such conditions would become impossible.' (Pasteur, 1885).*

(11) Aseptic animal; *a relative concept depending on the means of detection used. It is possible, for example, that some viruses cannot be detected owing to the absence of cytopathogenic action on cells used in tissue-culture.*

(12) *Robbins, Enders and Weller (1949) demonstrated the possibility of growing the virus of poliomyelitis on cultures of tissues other than those of neural origin. From then on, the use of these techniques in virology has become widespread.*

These two mice show cancer of the flank. (Photo Lod).

the ageing of the organism, and the exact needs of animals for food.

With the possibility of producing aseptic animals free from any detectable micro-organisms and the creation of inbred stock of a stabilised and known genotype, the modern biologist possesses an animal material very close to the ideal biological reagent.

Cell culture

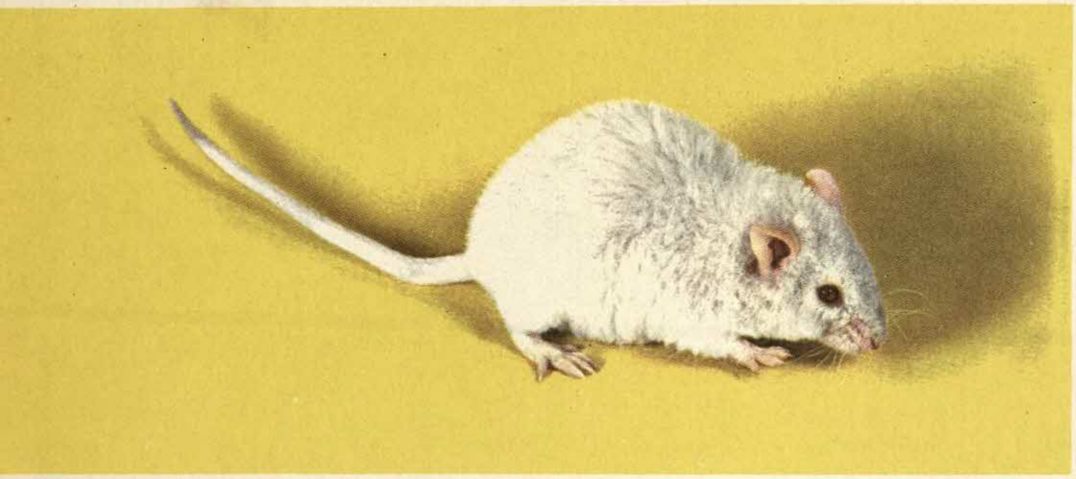
With a view to replacing higher organisms by a more stable living material, many other new techniques have been developed. Use of tissue-culture, known for a long time, is now widespread in virology; the possibility of using animal cells apart from the organism eliminates the intervention of variable factors relating to food, genetics and immunisation of the host.[12] In research on nutrition, new techniques have also been developed using micro-organisms which have in common with the higher organisms a need for food, in particular for vitamins and amino-acids. Such techniques consist basically in giving to the micro-organism a culture medium which contains all the ingredients for growth except that which is the subject of the analysis. The measurement of this growth gives a quantitative evaluation of the product to be analysed.

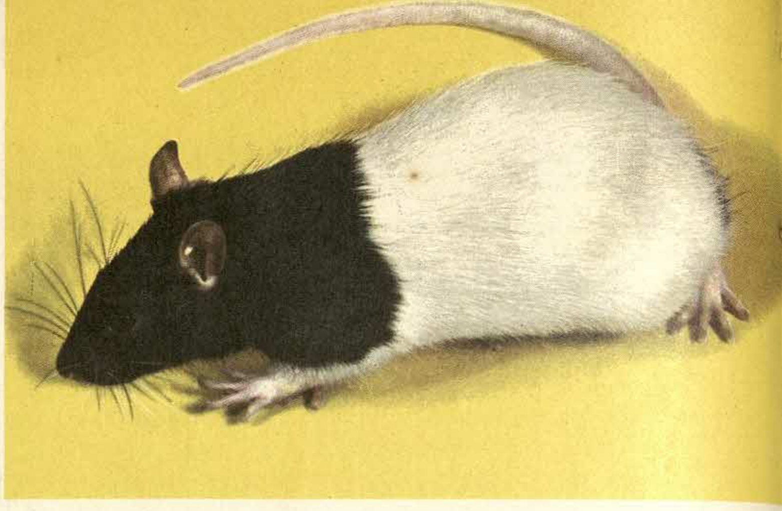
Animal cells, bacteria and yeasts used in these techniques have a great advantage over higher organisms, as they can be developed in a synthetic environment which is defined in detail and can be maintained in an incubator in a localised climate which is easy to control.

So the requirements of modern biology have led experimenters to develop new techniques which reduce as far as possible the variability of living material. That of genetic origin is obtained by in-breeding, but it seems that there may still be much to do in the control of variability due to environment. The techniques governing the production of aseptic animals already represents, in this field, a considerable advance, but these animals are still under the influence of many environmental factors which are variable and difficult to control in the case of the higher organisms.

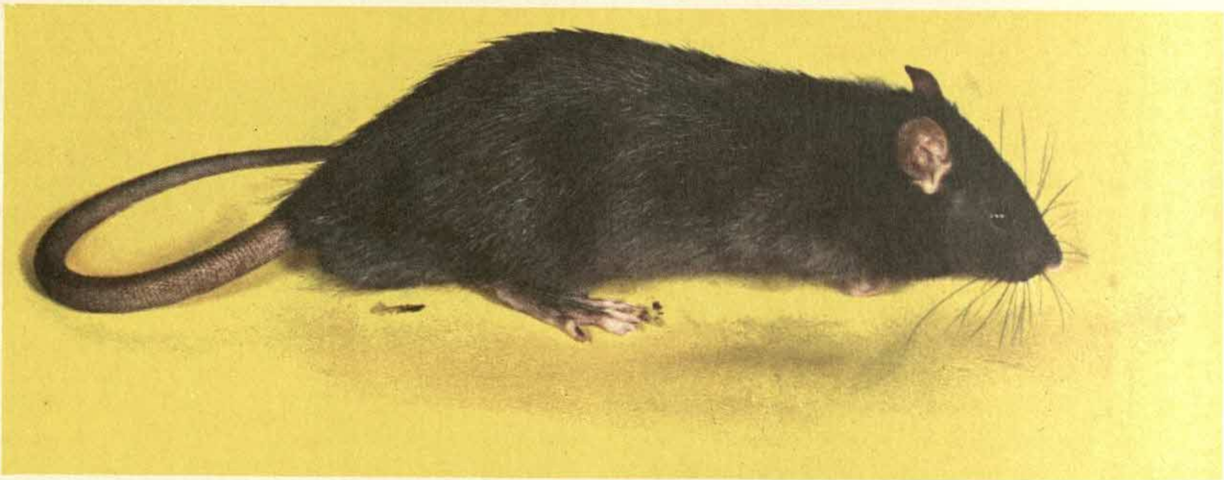
Does this keen interest shown by biology in new techniques mean that the era of the old laboratory animal is closed? Probably not, but the main concern of the modern biologist is to have well-known, stable, constant, living material, in other words to have a reliable biological reagent.

Experiments on heredity: this albino mouse, with its fine coat and sparse and crisp hair, makes it possible to study the influence of a special genes ('short-ear') which mainly affects the size of the external ear.



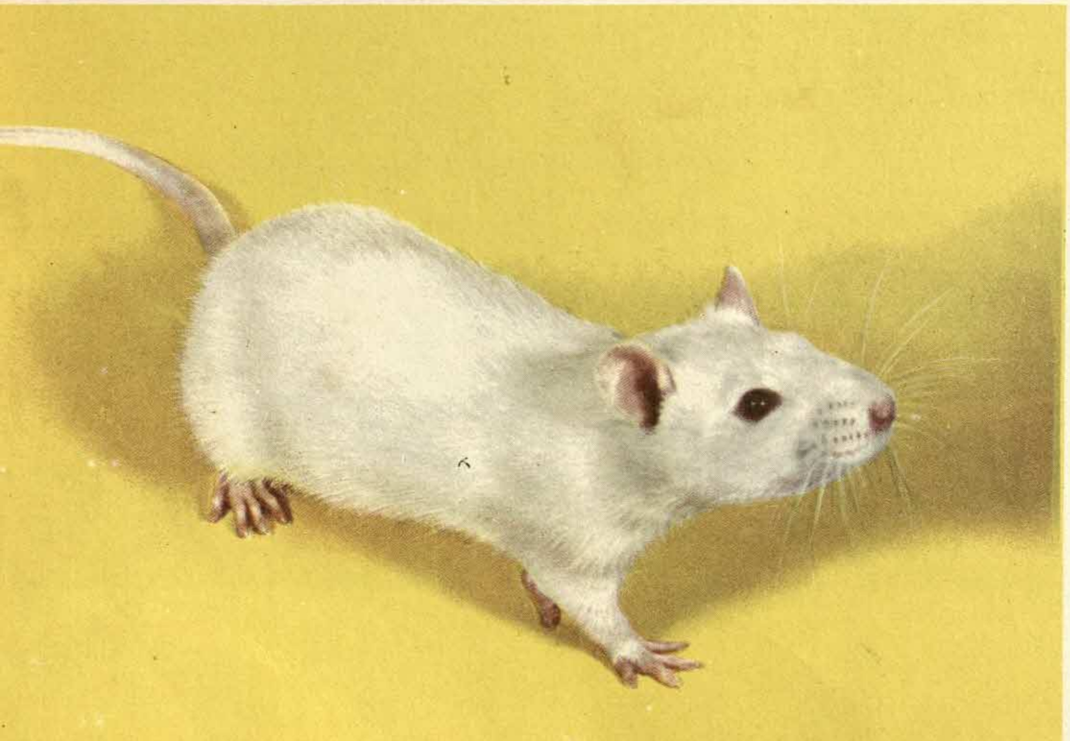


Biologists have carried out on this rat, of P.V.G. stock, experiments relating to the problems of nutrition and animal psychology.

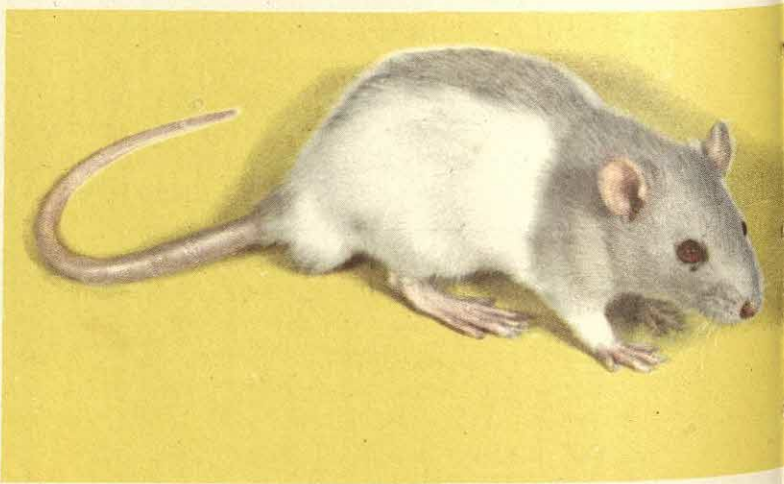


This rat, known as London Black, arises from a cross between a wild male (agouti colour) and an albino female. It differs from the wild black rat, Rattus rattus. *All laboratory rats are descended from the* Rattus norvegicus.

Albino rats (Wistar stock) developed in Philadelphia. Biologists all over the world use them because of their polyvalence and perfect adaptation to conditions of life in the laboratory.



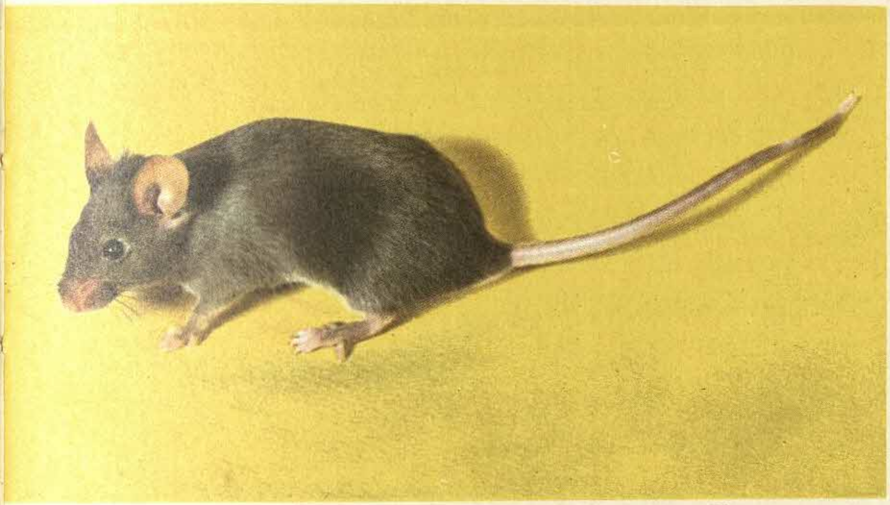
The August rat, with light brown hair and pink eyes (due to genes h and p) used in cancer research: it reacts to methylcholanthrene by the formation of tumours.



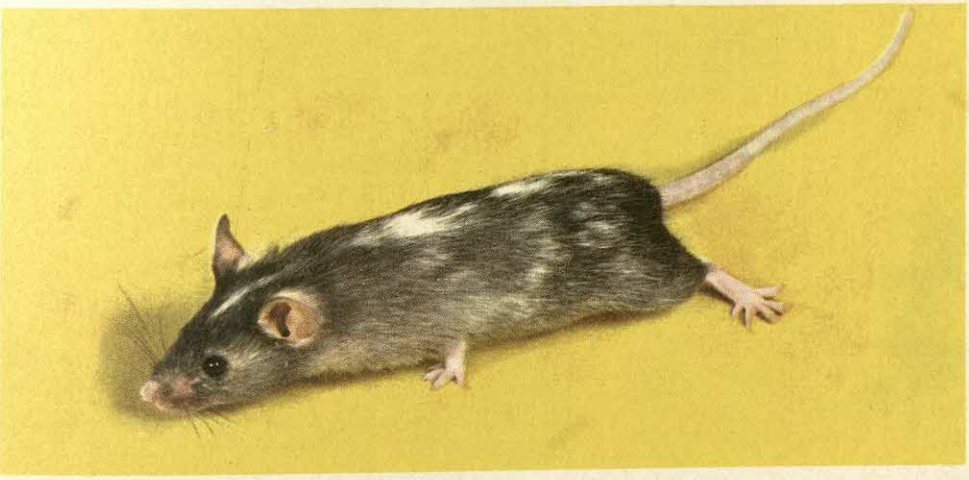
Laboratory animals

STATE INSTITUTE OF EDU
BANIPUR

The laboratory animal is above all else an organism studied for its reactions to various agents: inoculation of germs, chemical and biological substances, physical treatments, etc. It is a biological reagent. In some species (rats, mice) the needs of research have produced many specific breeds, obtained from individuals showing spontaneous characteristics of biological interest, whether in the field of heredity, mutations, or sensitivity to carcinogens. (Photos Lod).

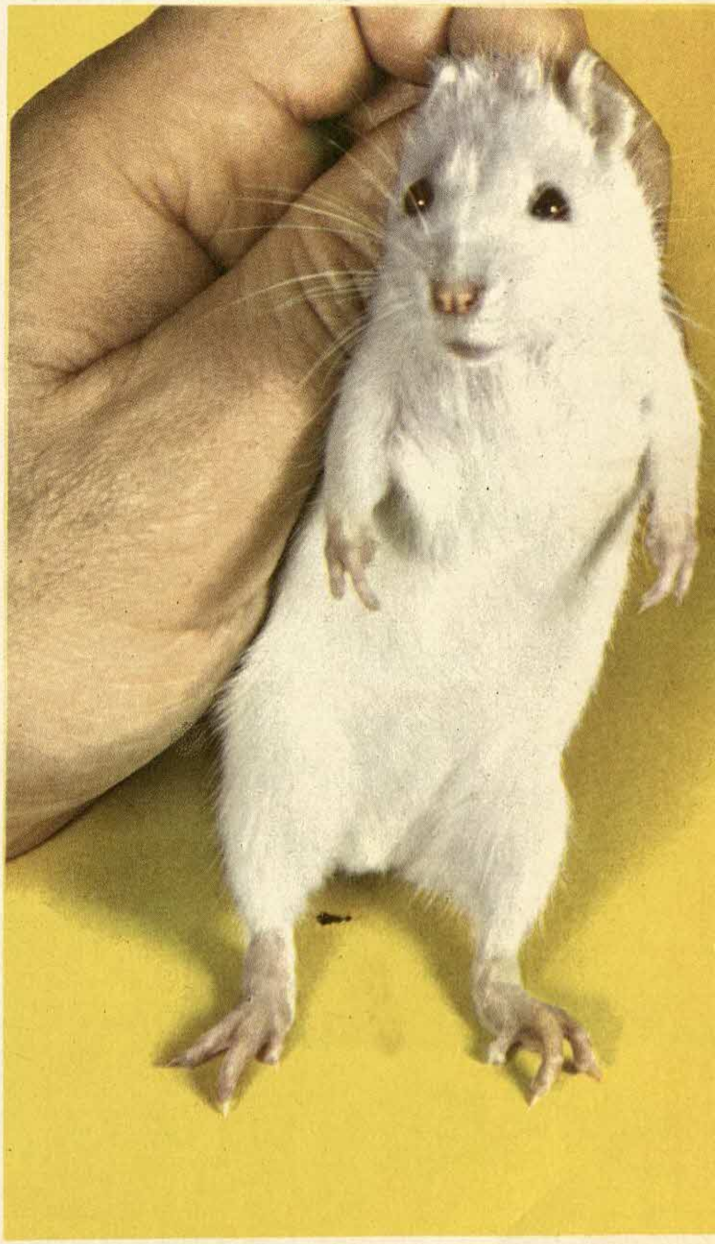


A mouse with a grey-coloured coat and black eyes belonging to stock C57B1, from which it was separated at an early stage. It is used for research on the suprarenal glands and in the field of haematology.



A black and white-coated mouse which is characteristic of a gene which is influenced by other modifying genes. The mutation appeared spontaneously in a family of the C57B1 breed.

A 'hypodactyl' rat: this spontaneous mutation, seen in the Wistar breed (developed in Philadelphia) affects the number of fingers on the four limbs. The males are sterile, the breed being maintained by heterozygous mating.



Chemical war on insects

Paul PESSON

Chemical warfare has found a peacetime vocation in protecting mankind against insects: the blood-sucking insects which spread disease, and the even larger number of insect species which damage his crops and bring illness to his farm animals. Gradually the scope of the chemical war has been extended through the development of specific substances (molluscicides, acaricides, nematocides)[1] *which will kill parasites without harming the host. And it has been extended still further to serve as a defence against harmful vertebrates, particularly rats and certain birds. Without these chemical pesticides, the world would be unable to produce the quantity of food needed to feed its population.*

The weevil larva does great damage to grain and cereals in warehouses. (Mag. × 12. Photo Lod).

Insecticides may act on an insect by causing severe cellular damage to a particular organ, or they may work in a more subtle, but no less effective manner, by upsetting the animal's physiological organisation, usually by blocking enzymatic functions which are indispensible for the life of the cell. The arsenicals, for example, provoke basically intestinal lesions, nicotine acts on the functioning of the heart and the nerves; Pyrethrin and DDT are neurotoxic compounds; cyanides block cellular repiration by acting on cytochrome enzyme oxidase; the phosphoric esters inhibit the enzyme cholinesterase and thus block the transmission of impulses along the nerves. However, many insecticides act simultaneously on several organs and on several important and vital functions. But it would be difficult to classify the innumerable substances used as insecticides according to their mode of action; for the study of the toxic effects of these substances on insects is still not very far advanced, and even the basic physiology of insects is largely unexplored. The need to discover the mode of action of insecticides, has in fact stimulated research in insect physiology.

Initially attention was directed mainly to the polyvalent insecticides, that is to say, those which are lethal to all insects. Today, however, research workers are concentrating on the search for specific insecticides, strictly devised for the destruction of particular undesirable insects, and on discovering the reason for this specificity. As a result of the introduction of DDT and other synthetic and organic insecticides which are toxic to most insects (and also to arthropods) the disadvantages of such polyvalent insecticides became clear.

The almost total destruction of all the entomological fauna in a cultivated zone was frequently found to be detrimental. Thus the destruction of pollinating insects (honey-bees, wild bees and other insects) reduced considerably the harvest of seeds or fruit, and the elimination of auxiliary insects, predators or parasites of harmful insects and arthropods led to the rapid multiplication of species which until then had been held in check by the law of biological equilibrium. Also, since the poisons were not specific, groups of resistant insects soon found that they were at an advantage throughout the world and rapidly spread. Today the problem of insect resistance to DDT and similar poisons has become a major one.

The specific action of insecticides confined to a small number of species is difficult to reconcile with the actual toxic properties of those products on living cells. In choosing an insecticide for a particular purpose one can only select that substance which is most effective against the unwanted insects and, simultaneously, least injurious to man, domestic animals, auxiliary insects, and the plant itself.

Analysis of the reasons why a chemical should show differing degrees of toxicity as between different insects and between insects and vertebrates is beginning to indicate the direction in which research workers must look in their search for new specific insecticides. It has been discovered, for example, that organic phosphorus insecticides may undergo two different fates in a living organism. They may be combined with water by the process called hydrolysis and converted into non-toxic products, or on the contrary they may be oxidised to produce a compound even more toxic than the initial product. These insecticides are, in general, very toxic to man, but it transpires that one of the compounds having these characteristics, a substance called malathion, is less dangerous because in man it is hydrolysed more rapidly than it is oxidised, whereas in the insect the reverse is true.

But it is largely by considering the route by which the toxic substance is introduced into the animal that it is possible to predict which species it will be particularly effective against. Insecticides can penetrate an insect's body through the mouth (ingested insecticides), by the respiratory pathway (asphyxiants or fumigants), or through the skin (contact insecticides). The last two categories ought, at least in theory, to affect all insects, regardless of species, which have breathed them or come into contact with them. Their specific action, if any, should be restricted to differences between species in sensitivity to the poison itself.

However, in practice this is not quite true. Some contact insecticides can be distributed in such a way that they are specific, simply because only a limited range of species have habits which would bring them into contact with the poison. For instance, the floating powders with a DDT base, used in the fight against mosquito larvae, are dusted onto the surface of the pools. When the larvae come to the surface to breathe, their breathing tube comes into contact with the powder and other aquatic animals which breathe air (such as the water boatman and pond skater) would be harmed by the insecticide powder. Those which do not come to the surface to breathe but are provided with gills (such as the Mayfly larva, the newt tadpole, the dragon-fly larva, and the blood-worm) are in general, unharmed.[3]

Contact insecticides can occasionally act as ingested insecticides and their effect can be limited by using powders in which the chemical particles are 'dressed' with a protective covering. Contact with this coated powder, or ingestion of it is normally harmless. But plant-eating insects, with crushing mouth-parts, tear off the coating and ingest the poison; the Hymenoptera, pollinisers and other desirable animals are unharmed.

Systemic insecticides

Spectacular progress, in selective action, has been achieved in the systemic insecticides. They are substances which are harmless to plants but highly poisonous to insects. The systemic insecticide is administered to plants like a medicine by spraying on the leaves, into the soil round the roots, or by the impregnation of seeds. When it has been absorbed into the plant it is transported by the sap, and quickly spreads to every part, even to points far removed from the point of application. Inoffensive to the plant, the toxic substance confers on it a protection against various parasites. This method has the virtues of giving protection to all parts of the plant, even those which have developed since the date of application.

This type of insecticide is very effective against all insects which bite and suck the sap (greenfly, cochineal, etc.). Insects which do not eat plants remain protected and even the predators and parasites of the sap-drinkers are not affected.

It is usual to avoid spraying those systemic insecticides which are also toxic on contact. Instead they are buried in containers close to the roots of the plant they are to protect. The containers are so designed that they decompose by bacterial action and release their contents into the soil over a period of time.

Since systemic insecticides can enter the plant through the roots, the leaves or the germinating seed, they can often be applied at the same time as other substances. For instance, they can be mixed with fertilizers and spread on the soil, or sprayed on leaves. Or it may be possible to combine them with chemical weed-killers.

CHEMICAL COMPOUNDS USED AS INSECTICIDES

I. *Fumigant Insecticides*

Sulphur dioxide
Ethylene oxide
Carbon bisulphide
Hydrocyanic acid
Methyl bromide
Carbon tetrachloride
Trichlorethylene
Para-dichlorbenzene
Chloropicrin

II. *Mineral Insecticides*

Arsenic and derivatives of arsenic:
  sodium arsenate
  lead arsenate
  arsenates of lime
Fluorides and fluorosilicates (barium fluorosilicate)

III. *Organic Insecticides of Plant Origin*

Nicotine
Pyrethrum and pyrethrins
Rotenone

IV. *Organic Insecticides of Mineral Origin: mineral oils*

Petrol and its derivatives:
  kerosene
  colourless oils
Oils from coal:
  anthracene oil
  creosote oil

V. *Synthetic Organic Insecticides*

(*a*) *Organic halogen compounds*

DDT
Lindane
Aldrin
Dieldrin
Chlordane
Heptachlor
Toxophene

(*b*) *Organic phosphorus compounds*

Tetra-ethyl-pyrophosphate (TEPP)
Hexa-ethyl-pyrophosphate (HEPP) 'Bladan'
Parathion
Demeton (Systex)
Diazinon
Malathion
Schradane or OMPA
  (octamethyipyprophosphoramide)

(c) *Organic sulphur compounds*

Thiocyanates and isothiocyanates
Polychlorocyclohexanes
Phenothiazine

Sometimes used to combat other species (see 'The Intensive Raising of Ants'), ants are nevertheless harmful insects which invade houses, spoil harvests, and pillage food reserves. (Mag. × 40. Photo Lod).

The widespread use of fertilizer-insecticides can bring about a serious imbalance amongst the microfauna of the soil which is indispensable for the formation of humus. It is not simply systemic insecticides which introduce this risk. Contact insecticides used to kill the larvae of subterranean insects (maggots and beetles) also destroy innumerable acari (mites) and collembolans (springtails). Investigations are going on to evaluate the role of these microarthropods and to discover a means of protecting them.

The persistence of insecticides

The length of time an insecticide remains active is an important factor in its usefulness in protecting crops: but a persistent insecticide may be a greater danger to man, domestic animals and useful insects. One of the great advantages of DDT, lindane, and several other synthetic chlorinated hydrocarbon insecticides, compared with other contact insecticides such as pyrethrins, nicotine, and rotenene, is their great persistence. Their long-lasting character has been put to good use in the battle against the anopheles mosquito, the carrier of malaria. Apart from the attack on the larval form by dusting the surface of ponds, the long-lasting contact insecticides are used for spraying houses to kill adult mosquitos.

Certainly these insecticides are not very dangerous to man in the dose normally used against insects. But precautions must be taken in the preparation of formulae-pastes, liquid emulsions and powders, from more concentrated material which is, of course, more toxic. Insecticidal sprays and extremely fine powders are more dangerous because they may be inhaled. The most serious risk, against which precautions must be taken, is that of chronic poisoning from absorbing the insecticide in food prepared from contaminated plants. Contact insecticides like DDT, which is between 500 and 1,000 times more toxic to insects than to man (lethal dose for the fly, 0·6 mg per kilo of body weight, against 250 to 600 mg per kilo body weight for mammals) can nevertheless accumulate in the fatty tissues with serious results. It has been shown that cows fed on forage previously treated with DDT, accumulate the insecticide in their milk. The cream in particular, is rich in DDT and so is butter made from it. The level of DDT in the cream can reach 68 parts per thousand, whereas the residue normally tolerated in food should not exceed 7 parts per million. Calves fed with this milk can show fairly serious signs of poisoning.

The long-lasting effects of insecticides, although advantageous in some cases, can prove inconvenient even in regard to insects. A high residue level is certainly useful for the protection of stored goods and of houses against undesirable vermin (moths, cockroaches, beetles, mosquitoes, ants). Walls, floors and furniture can be treated with insecticide paints and polishes which remain active for long periods. The same is true of the insecticides used to impregnate paper, carpets, wood (against termites) and fabrics (against moths), etc. But the residual effect of the insecticide may be an embarrassment to the farmer who has to spray the flowers of his fruit trees. Unless he is careful, the insecticide which prevents the fruit from being maggoty by killing the insects which come to lay eggs in the buds or flowers, will prevent it from forming at all by killing the useful pollen-gathering insects. This is why the date of applying the treatment is so important and should be carefully assessed. In many parts of the world crop-protection authorities in each area announce the expected date of appearance of the harmful insects and prescribe the periods of treatment.

(1) *Nematodes are very small cylindrical worms. Several species are parasitic on plants: they invade the ripening corn and provoke blight in it. Another nematode attacks the roots of beetroot. The substances which destroy nematodes, mites and parasitic molluscs, are called nematocides, acaricides and molluscides, respectively.*

(2) *The Chinese protected their crops against infestation by certain harmful insects by dusting their plants with fine sandy earth from the roads. Recent research has shown that non-toxic powders (inert powders) can themselves have an insecticidal action by abrading the fatty covering of the insect's integument (thickness about one micron), and thus causing severe loss of water from the tissues which proves fatal.*

The appearance of some pests takes place before the blossoming period, while some appear afterwards. In the first case it is more convenient to use insecticides of short durability which will cease to act during full flowering. In some instances it is the newborn larvae hatching from the egg which must be destroyed quickly, for once it penetrates to the centre of the flower or fruit, it cannot be attacked except by systemic insecticides. This is not always practicable because there may be no suitable systemic for that particular variety of plant. In all events a treatment applied too early or too late can be completely ineffectual.

Another factor limits the use of insecticides in the fight against parasites of cultivated crops; it is the eventual toxicity of certain of the compounds to various species of plants. DDT, for example, is harmless to the majority of plants, but it cannot be used to treat plants such as the melon, marrow, cucumber, or gourd which are sensitive to it. More often it is the oils, wetting agents and similar substances added to the active compound to make pastes or liquid emulsions, which are harmful and can destroy leaves, blemish fruits, etc. For these reasons, when a chemical product which appears to be an efficient insecticide is discovered a large research programme is required to find out its stability, maximum efficiency, ease of preparation, ease of application, non-toxicity to plants, etc.

The different techniques

Progress in the chemical battle has consisted not only in perfecting a number of efficient insecticidal chemicals but in perfecting the method of application. A wide range of products in different forms and different formulations have been developed; pastes, moistened powders, floating powders, solutions and emulsions. Application is mainly by powdering or spraying.

Considerable progress has been made in the techniques of dusting by the development of aerosol or atomising equipments which create more or less stable mists and require only small quantities of liquid.

Fumigation and baits

One must not confuse the techniques of distributing insecticide by smoke or mist with fumigation, which is the use of insecticides that are volatile at ordinary temperatures. These include naphthalene and paradichlorbenzene, familiar products used for protecting clothes against moths. Such fumigants are only effective for the disinfestation of air-tight places and cannot be used in the open air because of the rapid diffusion and dispersal of the insecticide vapour. However, techniques have been perfected for fumigation under fruit trees. Fumigants incorporated into soil are also used to control certain insects or their soil-dwelling larvae and especially nematode parasites of plants which always pass through a free infective stage in the soil. Fumigation is most widely used for disinfestation of holds of cargo-ships, silos containing cereals, and similar bulk stores.

Finally, as a means of adapting insecticide treatment to the biology of the insect to be destroyed, one sometimes uses insecticide baits, the poison being mixed with food or other substances which attract the insect. For instance, grains of rice or barley coated with barium fluorosilicate have proved efficient bait for the cricket; bran poisoned with metaldehyde attracts and kills slugs; while bran poisoned with lindane and spread from

(3) *In the same way the size of the particles in aerial dusting powders or liquid sprays influences their insecticidal efficacy. It has been discovered, for example, that the optimum dimension of droplets in a liquid spray is 22 microns for the destruction of flies and 16 microns for the destruction of mosquitoes which are smaller.*

Aphids are insects that live on the sap of their host plants. But the aphids are themselves parasitised by ants which rear them like livestock for the sticky juice they exude. The photograph shows ants and aphids on the branch of a rose bush. (Mag. × 40. Photo Lod).

Right: The bark of old trees is riddled with innumerable holes where harmful insects live, such as the sap-sucking white larva shown here. (Mag. × 20. Photo Lod).

aircraft in the path of bands of migratory locust larvae has proved effective. Sometimes a non-edible coloured bait which attracts the insects may be used instead. Dark brown strips of material impregnated with DDT behave as coloured bait for the tsetse fly and have proved effective when laid around water holes in tropical Africa.

The chemical armoury is completed by substances which either attract or repel particular insects. Some success has already been achieved with mosquito repellents, which can be applied to the skin and clothes, being based on dimethylphthalate and related compounds. Further research will probably lead to the discovery of substances which attract particular insects. If these can be combined with insecticides this will help to make them more specific in their action.

The principles involved in the chemical control of insects apply equally to the control of other enemies of man. A number of pesticides are widely used against harmful vertebrates, particularly rats and certain birds, such as rooks and crows. For many years the method of control consisted in mixing toxic substances (oral poisons such as strychnine, zinc phosphate, etc.)[2] with suitably chosen bait. It is possible to use poisons which are less toxic to human beings and domestic animals: but these are also less palatable to the rodents, which are crafty enough to avoid them.

The war against these animals has gained from progress made in the control of insects: certain insecticides, such as endrin and parathion, have been sprayed from the air to destroy rural rodents and grain-eating birds. Some raticides, like the derivatives of coumaine, can be used in the same way as the contact poisons; the rats, on licking their coats, absorb the poison, which is cumulative and in due course they absorb sufficient to bring about internal haemorrhages from which they die. Voles and field mice are being brought under control in another way; by spraying the areas in which they are swarming so that the poison is deposited on the vegetation they eat. The same basic control methods can be extended to the fungal, bacterial, and virus diseases of cultivated plants (using fungicides and bactericides) and even to the destruction of weeds and other unwanted plants (stinging nettles, thistles, brambles, broom, couch grass, rushes, sedge, etc.) for which specific herbicides have been developed.

A scientifically conducted war

Chemical control must always be conducted in a scientific manner to ensure that it is fully effective and introduces a minimum of hazards. The choice of pesticide, the method of using it, and the whole biological background of the application needs careful study.

It is also necessary to ensure that the method is not abused. Insects, rats and many pests are so prolific and have such immense ability to survive that there is no question of destroying them once and for all. But serious damage may be done to useful species with less capacity to survive. Because most pesticides are poisonous to a wide range of animals, their use requires special care to avoid harm to man and domestic animals, and also to safeguard wild-life, the role of which is not fully understood.

The basic precaution which must be taken is strict supervision of conditions of use, and in particular the length and date of treatment. The useful fauna need to have reserves in which they can live peacefully without interference from chemicals, if they are to maintain themselves. It is therefore advisable to avoid blanket spraying of areas and to leave untreated uncultivated areas in farmland which can act as refuges—hedges, fallow land, warrens, etc. Spraying from the air is particularly harmful because it leaves few such untreated areas, and can thus reduce greatly the population of insect-eating birds especially when forest land is sprayed. Already the number and variety of useful animals has dropped noticeably following the spread of single-crop cultivation over large areas. Their complete disappearance would be a disaster.

But the chemical battle against pests must not be a blind war which exterminates all living things from our woods and fields. Used intelligently and with an understanding of the biology of the fauna, it can control the pest without damaging greatly the many other creatures which play useful or indispensable parts in the pattern of nature. This fauna is a natural legacy and we are neither sufficiently rich nor sure of ourselves to risk its loss by the indiscriminate use of chemical poisons.

The biological struggle

Pierre GRISON

> *'Some species are necessary as prey and others as predators and brakes on propagation. One cannot rationally conceive a state of things where there were flies without swallows, and vice versa.'*
>
> CUVIER

> *'Biological control is the name given to methods of destroying harmful insects by the rational use of their natural enemies in either the animal or vegetable kingdom.'*
>
> BALACHOWSKY

The object of this chapter is to make readers aware of how biological equilibria are established in nature and why it is dangerous to interfere with them, as for instance by some methods of pest control. The interdependence of the vast variety of living things which inhabit every corner of the world is not usually apparent to the layman except during certain catastrophes.

Insects are the most numerous inhabitants of our planet, and make up three-quarters of all known animal species.[1] They are involved in particularly large and complex interrelationships with other insects, plants and animals, and therefore play a very important part in the whole assembly.

The vegetation would have disappeared from a large part of the earth's surface, if the rapid multiplication of plant-eating insects had not been held in check by other insects and parasites of various kinds. These parasites often themselves have hyperparasites[2] which in turn control the population of their hosts. This results in multiple and complicated relationships.

Under these conditions of complex interdependence disturbance of a single biological factor is in danger of upsetting the whole, in exactly the same way that removing a single card from a house of cards is likely to cause the collapse of the whole structure.

It is impossible for man to understand a *priori* the multiple interactions of the different elements of this biocoenosis,[3] or even to analyse all the possible effects. But he learns from practical lessons and when the plants which are useful to him undergo attacks from pests he tries to use the natural agents which ensure 'ecological regulation', that is to say, the control of the plant and animal population within the biocoenosis.

Biological unbalance

It is beyond doubt that the artificial introduction and extension of a species of plant as an agricultural crop in an area previously occupied by a natural population results in the disappearance not only of the wild botanical species which live there but also of the animal species, and notably the insect population. All types of cultivation upset the natural equilibrium. A notable case was the spread of the potato in North America during the middle of the nineteenth century as emigrants spread westwards across the United States.

When the settlers reached what is now Colorado and Arizona, the cultivated potato plants they had brought with them met wild *Solanum* species on which there lived, more or less harmlessly, an insect called the doryphore (*Leptinotarsa decemlineata*). It quickly transferred its attentions from the wild *Solanum cornutum* on which it had lived to *Solanum tuberosum*—the potato—newly acclimatised to this region. On its new plant-host the dory-

(1) *Insects inhabit many different environments and eat a wide range of foods. Plants may serve as support or food. Insects which eat vegetation exclusively are called phytophages. Those which live on a diet of phytophagous insects are called entomophages.*

(2) Hyperparasites: *entomophagous insects which parasitise another entomophagous species. When the latter is a parasite on a phytophagous insect, the hyperparasite is said to be of the second degree; but when the host-species is itself a hyperparasite there is tertiary, quaternary or higher order parasitism.*

(3) Biocoenosis: *a community of animal species which lives in a given habitat, of a composition which is relatively constant for any given area (Marcel Prenant). This restricted habitat, or* biotope, *comprises the plant population where the species of insects proliferate and can be differentiated. Some only attack one species of plant (monophagous) others have more varied tastes (oligophagous), whilst some eat everything they encounter (polyphagous).*

(4) Predator: *carnivorous entomophagous insects which attack, kill and devour other insects, called the prey. By contrast, a parasite is an entomophagous insect the larvae of which develops at the expense of another living insect called the host, which it kills only after the larva is fully-developed.*

(5) Biological equilibrium: *the state in which the 'level of population' of several species undergoes only small fluctuations in the course of time because of the interdependence of the species and the reciprocal action that one exercises on the other.*

phore multiplied in a remarkable fashion and, following the route already taken by the potato (although in the reverse direction) made its appearance on the east coast in 1874.

The result was disastrous for the potato crops because the parasites and predators[5] which in its original home had kept the population of doryphores in equilibrium with the primitive plant-host, did not follow the insect eastwards. Instead, the farmers used chemicals to kill the Colorado beetle, as the doryphore was now called, and Paris green or copper acetoarsenite first enriched the agricultural pharmacopoeia.

The extension and industrialisation of agriculture led the farmers to remove all traces of wild life which had acted as refuges for the parasites and predators of insects dangerous to plants. Thus in clearing hedges and brushwood around villages and farms, the olive growers of the Mediterranean basin also destroyed the parasites which formerly restricted the proliferation of the olive fly (*Dacus oleae*).

Thus, modern methods of plant-protection ended by modifying the biological equilibrium.[5] The synthetic organic insecticides which have brought about such striking victories against certain pests, present a serious danger, especially when sprayed from the air without being confined strictly to cultivated zones, because uncultivated regions sprayed accidentally in this way may remain without any animal life for a considerable time, depending on the period during which the toxic material remains active.

In addition, entomologists have discovered that important insect-eating species such as many Hymenoptera and Diptera are more sensitive to the action of insecticides than most of the plant pests against which they are directed.[6]

This state of affairs is worthy of serious thought. In Spain an effort to control Gipsy moth (*Lymantria dispar*), which attcks oaks and cork-trees, led to the destruction of the auxiliary fauna, notably the parasites of the species *Tortrix viridina* which proceeded to multiply; in fact, it replaced the *Lymantria* caterpillar as the destructive fauna of the oaks which it was originally intended to save. Since *Tortrix viridina* has the habit of burrowing into crevices it was protected from chemical insecticides, and finally, through ignorance of biological equilibria, a known pest was replaced by a new one which was more difficult to combat.

The case of *Lymantria dispar* is equally remarkable for the fact that in regions which have not been subjected to intensive chemical attack, it causes damage only in two or three years out of a cycle of ten or fifteen. Research is still continuing on the way in which biological equilibria can be upset with resulting multiplication of a pest. But it is in the natural order of things that when the multiplication of the pests is at its height the predators themselves multiply rapidly and almost completely suppress the phytophagous pest.

For example, in Corsica, in 1954, a predator, a Coleopteran beetle (*Calosoma sycophanta*) multiplied during a single season to such an extent that the caterpillars of *Lymantria* were completely annihilated. An important problem remains to be solved: the predators may be so effective that, having annihilated the pests, they are then unable to maintain themselves.

The natural re-establishment of biological equilibrium

Examples of re-establishment of natural equilibrium by the introduction of a natural enemy of the pests are significant. The cochineal of orange-trees (*Icerya purchasi*), introduced accidentally into California without its predator the lady-bird (*Rodolia cardinalis*), which curbs its development in Australia, led to catastrophic damage. The disaster was ended by the systematic introduc-

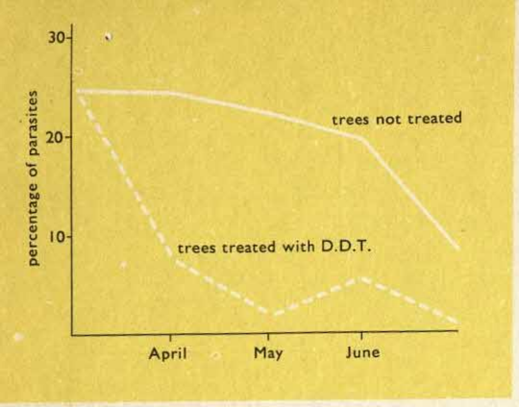
The golden 'sergeant' or 'gardener' beetle is one of the most beautiful found in temperate Europe. It is common in gardens and fields where it feeds on harmful insects and even attacks slugs.

(6) *Sensitivity of different insects to chemical insecticides: the proportion of different orders of insects destroyed following an aerial application of lindane directed against the cockchafer. Diptera (eaters of insects and hosts) 48%; Hymenoptera (eaters of insects) 21%; Coleoptera (eaters of plants) 14%; Hemiptera (eaters of plants) 15%; Lepidoptera (eaters of plants) 2%.*

(7) *Analagous trials have been undertaken in Europe with a closely-related germ which causes 'milky' disease in the larvae of the cockchafer.*

(8) *Acclimatization of insects: difficulties in acclimatizing insects in their new surroundings are a common cause of failure in biological control. This is what happened in an attempt to control the oriental peach-moth introduced into the United States from Japan and Korea. Between 1930 and 1939 about 200,000 cocoons and 20,000 adult parasites of a number of species were collected. Entomologists placed great hopes on one of these*

Continued on next page



Insecticides, such as DDT, kill insects indiscriminately. The graphs show how the insect population of an orchard is reduced when it is sprayed with insecticide.

tion of the lady-bird and this method has since been used effectively throughout the world wherever the cochineal is found.

Similar results have been obtained with pathogenic micro-organisms. In 1944, the sawfly of the Norwegian spruce appeared in the province of New Brunswick, Canada, and did great damage to forest land. The outbreak was successfully controlled by introducing carriers of a virus disease of the sawfly which, in Scandinavia, keeps the pest's population to a relatively low level.

The virus, in this example is a very special kind of insect parasite; insects are parasitised not only by other species of insects but also by a wide variety of pathogenic micro-organisms: fungi, bacteria, viruses and even protozoa. These micro-organisms may multiply rapidly, causing outbreaks which lead to considerable destruction of the unwanted insects. They have been known to naturalists for as long as the predatory insects. However, they have not given satisfactory results in the biological war against pests because not enough has been known about them and the manner in which they spread through the population. For this reason, the first attempts to use bacterial or mycological diseases for pest control were disappointing.

Steinhaus, of Berkeley University, California, was responsible for re-introducing the microbiological assault on insects with the successful control of the Japanese cockroach by infecting them with *Bacillus popilliae*[7]. In the United States and Canada laboratories carrying out fundamental research are making progress in understanding the diseases of insects. In France the Institut Pasteur has carried out research on *Bacillus thuringiensis*, a pathogenic agent which is now cultured on a considerable scale and is employed against numerous lepidoptera which are harmful to crops.

An entirely different approach is the development of strains of plant which are resistant to attack by insects. Most of these special strains owe their resistance to the fact that they are immune to the virus disease transmitted to normal plants by the insect. In these cases the damage done to the plant is not due so much to the insect itself as to the infection it carries.

Methods and examples

The methods used for the introduction and acclimatisation of suitable pest parasites are in general the following: entomologists prospect the original home of the pests where they are generally in equilibrium with the fauna. Sometimes they visit nearby territories where species similar to the pest are found, for the organisms that keep these species under control may also be active in combating the pest and may even be more effective against their new host than against their usual one. Parallel with this work a survey is made of the possible harmful effect of the parasites on the harvest to make sure that introducing the newcomer does not bring fresh troubles.

When the necessary investigations are complete and a decision has been made on the best organism to use, the parasites are collected in the form in which they are least fragile. Great care is taken, even when they are transported by air, since it is essential to have living colonies. The destination is generally a special quarantine laboratory where the insects are first re-identified and then reared through at least one generation. This precaution is indispensable because the parasites may be carrying undesirable parasites of their own.

The work then divides into two parts: first, the stock of parasites must be maintained for permanent rearing, and, secondly, tests must be carried out to ensure that the insect can acclimatise itself to the territory where it is to be introduced. Maintaining the stock is fairly straightforward provided means are available for long-scale rearing of the host insects on which the parasites live.

The second part of the work requires laboratory trials to study the behaviour of the parasites under different conditions such as variations in temperature and humidity which may be encountered in the new environment.

When the quarantine laboratory is able to supply sufficient parasites, the first group is released into chosen areas at a time when, according to the laboratory tests, their chance of survival is greatest.

Acclimatisation generally presents two major difficulties[8] which have to be overcome by the parasites if the method is to be effective. The first is that of wintering. Often the parasites encounter climatic winter conditions in the new territory which are not

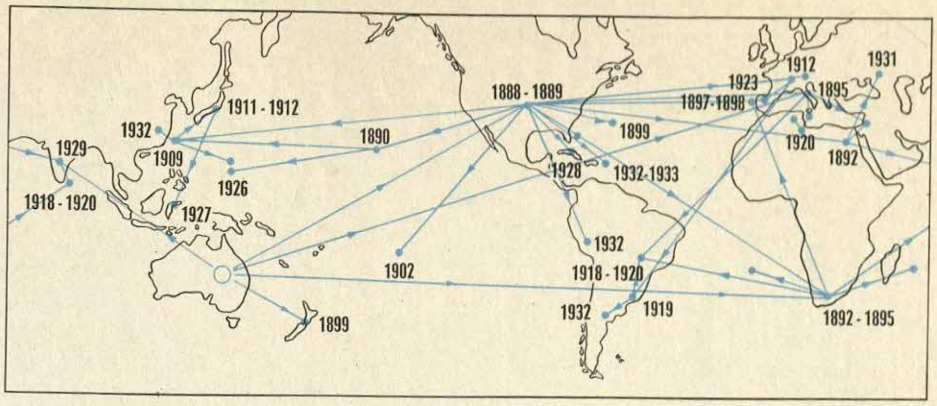
Continued from previous page

parasites Horogenes molestae *Uchida, which was raised in quantity and released into the Eastern States of America. However, it did not establish itself because there was no intermediate host within which it could pass the winter. Another species* Agathis diversus *Mues, introduced about the same time, has been able to exist for more than twenty years following introduction but has never built up a sufficient population to be effective.*

(9) *Rearing and release of parasites of cereal bugs. In 1955 the Laboratory for Biological Control in Ispahan raised 207 million* Microphanurus semistriatus *Nees which were released over 33,000 acres of infested fields in the regions of Ispahan and Chiraz. In fact, the biologists estimated that if there were two cereal bugs to a square metre it would be necessary to release 5,000 parasites per acre.*

(10) Sporulation: *the ability of certain bacteria to form spores composed of living material surrounded by a thick membrane when the environment becomes impoverished or conditions are unfavourable.*

(11) *The bulk production of this bacterium is easy in artificial culture. In various laboratories throughout the world, particularly in the United States, Canada, France, Germany and Czechoslovakia, studies have been carried out on the use of powders consisting of a mixture of bacterial spores and toxins, which can be dusted over cultivated areas in the same way as chemical insecticides.*



The female of the scarab beetle Rodalia cardinalis *was introduced into the United States from Australia in 1888. Since then this insect has crossed every ocean and is distributed over five continents and more than fifty countries. In 1892 it reached South Africa and Egypt, Italy in 1895, Spain in 1897 and New Zealand in 1899. By 1911 it had arrived in Japan and since 1920 has reached India, South America and Africa. (After Clausen, 1936).*

identical to those of their place of origin and which compromise their survival.

The second difficulty is in providing in the new environment conditions in which the parasites can maintain themselves over the whole of their life cycle. The pests which we intend to attack may be their hosts during a relatively short period of the year and an intermediate host may be needed to help the parasites to live and multiply at other times.

Thus American entomologists have applied another method of pest control based on the possibility of adapting a parasite infesting a given host to a new and accidental host. Where peach crops have been damaged by the caterpillar of the oriental moth (*Laspeyresia molesta*), attention was turned to another caterpillar which infests strawberries and is controlled naturally in the United States by *Macrocentrus ancylivorus*. Very large numbers of this parasite were raised and released from time to time in peach orchards suffering from oriental moth.

The indigenous *Macrocentrus ancylivorus* managed to withstand the climatic conditions of the Eastern American States and was very well able to survive the rigorous winters of those regions. But the change of host is not always easy to bring about because many entomophagous insects are so strictly conservative in their tastes that there is a specially adapted strain for each host.

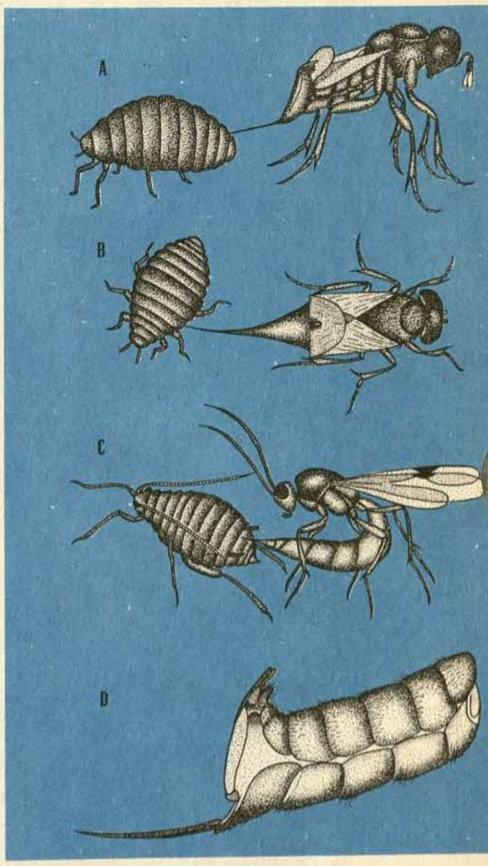
This frequently occurs with the oophagous parasite *Trichogramma evanescens*, which attacks the eggs of numerous species of lepidoptera. This parasite can be reared readily on the eggs of the corn moth, *Sitotroga cereallela* and entomologists hoped that it would enable them to control a number of other species of Lepidoptera which were important agricultural pests. Experiments with *Trichogramma evanescens* were carried out in the United States against the potato-worm and in various other countries against the minute caterpillars of sugar-cane; it is still used in Eastern Europe against several nocturnal Lepidoptera. However, the results have on the whole been disappointing because of this tendency of *Trichogramma* to specialise on particular hosts which reduced its effectiveness against the new host it was intended to attack.

Indigenous parasites restrict the proliferation of their insect hosts and so tend to maintain the biological equilibrium. But, in fact, any major change in parasite or host populations upsets the balance between the native insect species in an area. The parasite population does not rise quickly enough to match the increasing population of its host during an outbreak. Would it be possible, under the circumstances to reinforce the parasite population, and so recover biological equilibrium more rapidly?

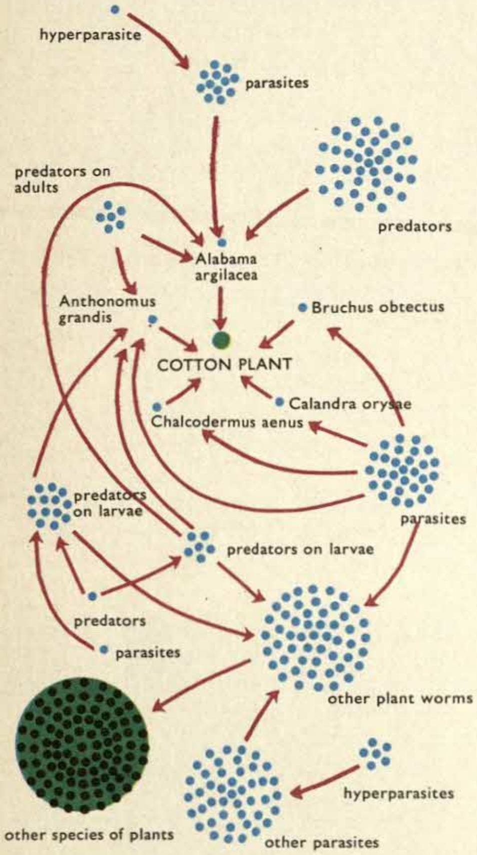
Decaux showed that this was the case by an experiment on the apple blossom weevil which he carried out in 1880. He gathered from eight hundred apple trees, fourteen bushels of blossom and buds infested with the weevil, and from these removed about 250,000 hymenopteran parasites of the species *Pimpla pomorum*. The parasites, when released in a weevil-infested orchard, checked the pest. The operation was repeated the following year and the orchard appears to have been protected from attack by the weevil for a period of ten years.

The International Commission for Biological Control has made efforts to encourage the preservation of indigenous parasites and to extend this method of pest control. Very often the use of pest parasites has failed or been only partially successful because the parasites have been introduced at an inappropriate time. If there is a gap between the moment when the parasites are released and the period when the pests proliferate, the parasite population may be weakened before it has an opportunity to attack the pests. Or the parasites may be introduced too late to prevent the ravages of the pest. The importance of timing is demonstrated in the case of the tachinid flies which are parasitic on the procession caterpillars studied by Biliotti at Antibes. He found that under normal conditions these entomophagous flies came out a little after the main period of development of the caterpillar. He concluded that if it were possible by appropriate rearing techniques to

(12) Polyhedral disease: *a disease of insects caused by the proliferation of certain viruses which are enclosed in polyhedral protein membranes. The viruses bring about the breakdown and death of the cells and tissues in which they multiply.*



Aphelinus mali: *Certain insects lay their eggs in the larvae of other species where they find food necessary for growth. A, B and C: egg-laying process. D: detail of laying apparatus.*


THE COTTON WEEVIL COMPLEX

The cotton weevil was introduced into the United States from Mexico without its natural parasites. These were later found (to the immense advantage of cotton growers) on a whole variety of plants. The complexity of biological equilibrium is shown in this diagram: 216 species of insects are involved in a delicate balance in an environment composed of 92 botanical species.

Opposite page:

For the human eye the animal world is not only the profusion of forms and modes of life to which the preceding pages have been devoted; it is also the harmony of line and colour to be admired in this group of egrets. (Zoological Park of Clères, Photo Lod).

encourage an earlier appearance of the tachinid flies, their action would possibly be increased tenfold.

An analogous procedure was put into practice against the bug *Erygaster integriceps*, which devastates cereal crops in Middle-eastern countries. The biological control of these bugs is normally effected by an oophagous parasite of the genus *Microphanurus*, which, however, suffers heavy mortality during the winter and therefore appears in nature before the period of intensive multiplication of its host. Laboratories were established in Iran[9] and other countries where the pest is prevalent to raise *Ergyaster integriceps* and its parasites in very large quantities.

The use of pathogenic organisms and radioactivity

Another type of parasite which is now proving effective in some forms of pest control is the pathogenic bacterium. One on which a great deal of fundamental bacteriological and entomological work has been done is *Bacillus thuringiensis* which produces a fatal infection in a wide variety of caterpillars. One of the ways in which the bacillus kills its host is by the production of a toxin or poison which crystallises at the moment of sporulation.[10] The toxin is ingested by the caterpillar, bringing about almost immediate paralysis of the digestive system or total paralysis of the body. The caterpillars soon stop feeding and destroying foliage and die in a short time. The sensitivity of caterpillars to the action of this bacterial toxin varies in different species and groups. Research workers have now isolated different strains of bacteria which show varying degrees of virulence against each group of Lepidoptera.[11]

This type of 'biological' insecticide, has immense advantages over chemical insecticides, since it is not poisonous to man or domestic animals and has little activity against bees and other pollinating insects.

At present, work is also being carried out on insect viruses, particularly those which promote 'polyhedral diseases',[12] and which may, therefore, be used as biological insecticides. These diseases have been known for almost a century, notably in the silk-worm where severe epidemics are well known to breeders.

Insect viruses are peculiar in that they form inclusion bodies,[13] the virus particles being protected by a capsule of protein which gives them extraordinary powers of preservation. But, like all viruses, they are very infectious when they are able to develop in a contaminated organism. They can be transmitted from one individual to another in various ways, in particular in the food the phytophagous insect eats. The viruses are used to control pests by spraying the leaves of crops, so that the likelihood of an insect being infected is very high. Canadian workers successfully used a specific virus of the sawfly of Norwegian spruce and in fifteen years there has been no recurrence of infestation.

Finally, a completely new process can be classed among the biological controlling factors since it has as its aim the disturbance of equilibrium in a population of harmful insects. This process is one of the many applications of atomic energy, since it makes use of radioactive cobalt (or any other source of radiation) to sterilize the males of harmful insects obtained by mass rearing. These males are then released and breed with normal females, without offspring, of course. If the insects are of a type that mate only once, and the number of sterilised males released is very large, the succeeding generation is small. The method is an application of statistical studies on populations. If sterilised males are released repeatedly there is in each generation a progressive and rapid diminution of progeny.

For the procedure to be successful the emergence and sexual maturity of the females must occur in nature several days before the appearance of the males; as the females can copulate only once in their lives, they would meet only the irradiated males, which have been released before the emergence of the normal males. These limiting conditions are not very frequent but they exist among certain mosquitoes and the screw fly against which the method has been used experimentally and with success by Americans.

Major advances in biological control cannot be expected until there is a considerable degree of international collaboration, which would enable problems to be distributed between different specialised laboratories, instead of each laboratory having to spread its workers and materials over a wide range of subjects requiring investigation.

Biological control offers many incontestable advantages: it is selective and therefore completely without danger to man, higher animals and the majority of fauna, other than the pests against which it is directed; and it helps to re-establish an acceptable natural equilibrium when woods and virgin land are replaced by intensive cultivation.

(13) Inclusion bodies: *infectious particles, peculiar to insects, composed of viruses or pathogenic germs and surrounded by a protein membrane.*

INDEX

Page numbers in italics refer to illustrations

abyssal regions 55, 56
adrenalectomy 73
aerial plankton 54, 55
amoeba *13*
amphibia *16*, 20
Amphioxus 19
anabiosis 59
androgens 84
anhydrobiosis 59
anisogamy 49
anthers 127
Apoidea 130
apple blossom weevil 157
apprenticeship 139
Apus 27
arthropods *15*, 18, 67, 69
artificial transducers 69
aseptic animals 144
Atta 115
autogamy 130
axolotl *33*, 37
bacteria 15
basophilia 62
batesian mimicry *120*, *121*, 125
benthic 55, 56
biocentic 154
biocoenosis 55, 56, 154
biological disequilibrium 111, 154
biological equilibrium 154, 155
biological insecticides 158
bipolar neurons 74
birds *19*, 20
blenny 36
Bonellia 49
bower birds 50
breed 143
Cambrian period 23
camouflage 120, 121, 122, *123*
cave-dwelling animals 57
cavity corpuscle 62
Cecropia 46
cell culture 145
Cephalochordata 19
Ceratites 28
Ceratodus 25, *27*, 28
chemical warfare 148
chemoreceptors 71, 72
chironomids 57
chondriosome 62
Chordata 18, 19
chromatin 62
chromosomes 32
Cidaris 25, 26
cilia 74
coadaptation 34
cockroaches *32*, 34
coelacanth 25, *27*, 28
coelom 17
coelomates 17
Collembola *26*, *36*, 37
complex cycles 53
conspecific 84
conspicuousness 124
constraint 140
convergence 35, 66, 122
copulation 52
corpus allatum 45, 46
cotton weevil *158*
counting birds 94, 95
cricket *45*
cuticle 44, 59, 72
cyclostomes 19
cytological transformation 59
dance 88
Daphnia *51*
D.D.T. 148-151
diploblastica 16
disguise 121, 122
disruptive colouring 122, 126, *126*
dominance 80, 81, 140
Drosophila *31*, 32
ecdysone 45
Echinodermata 17, 18
echo-location 68
ecological regulation 154
ecology 15, 17, 54
ectoparasites 105, 107
effector organs 66
Electrophorus 69
electro-physiological methods 72
embryonic layers 18
endoparasites 105, 107
entomophages 154, 156
epineuria 17, 18
Erithacus rubecula 77
extreme environments 53, 54
eyespots *68*, 126
false warning 125
fauna of the ocean troughs 57
fertilisation 51
fibroblasts 59
firebrats 43
fish *17*, 19
fleeing distance 140
Foraminifera *56*, 57
Formica fusca 135
Formica rufa 135
fossilized eel *29*
fumigation 151
genes 31
genotype 144
geocratic periods 54, 55
golden beetle *155*
Goniatites 24, 28
gustatory receptors 71, 72
hermit crab *106*
herring gull 76, 77, 78
heterozygosis 144
hierarchies 80
homochromy (similarity in colour) 120, *123*
homozygosis 143, 144
hyalinisation 62
hyponeuria 17, 18
imago *41*, 42
inbred stock 143, 144
inbreeding 143, 144
inclusion bodies 158
insecticides 148-152
Insectivora 20
insect viruses 158
intention movements 78, 84, 86
interpretation of messages 66
interspecific 84
isogamy 49
isolation 32
juvenile hormones 46
keyhole limpet *27*
lagena 25, *26*
latent form of life 62
laternal line 68, 69
life-cycle 53, 106
Limulus *26*, 28
locust *38-41*
mammals 20, *20*
mazes *97*, *99*, 100, 101
meiosis 17
messor 115
metamorphosis 42
metanephros 20
Metazoa 16, 17
mice *145*, *146*, *147*
microclimates 110
microvilli 73
mimicry *121*, *124*, 124, *125*
mitochondria 59
Mollusca 17, 20, *69*, 108
Monogenea 106
moulting (of locusts) *38-41*, 45
müllerian mimicry 125
mutation 31
mutation rate 32
Mystacocaridae 56
natural populations 53, 54
Nautilus 27, 28, *28*
navigation 112
nectar 130
Nemathelminthes 17
nematodes 59, 60, *61*
Neopilina 25, *27*, 57
neoteny 106
Nucleolites 25, *26*
Nummulites 16, 28
nymph 43, *47*
olfactory nerve 74
olfactory receptors 71, 72
oysters *21*, *27*
panchronic 25, *26*, *27*
panspermy 55
parallax 66, 67
parasites 105, 107
parenchyma 17
pathogenic organisms 158
pelagic larval forms 57
Periophthalmia 35
Peripatus *25*
persistence (of insecticides) 150
phylogenetic relationships 67
Platyhelminthes 17
Pleurotoma *27*
Pogonophora 18
polybies 114
polychaete worms 17, 18
polymorphism 44
Polystoma 106
predators 115, 154, 155
Primates 20
Proteus 37
Protopterus 61
psychological methods 72
pupa 25, *27*
radio-active cobalt 158
range of variation 54
rats *146*, *147*
releasers 75-77
reproductive potential 53
reptiles *18*, 20
revival 59
Rhodnius prolixus 45
Rhynchocephalians *27*
rotifers 17, 59, *60*, 61
rover-beetles 118
Salenia 24, *26*
selection 31
sense cells 65
senses 69
sensory organs 66
sexual dimorphism 49
sexual odours 71, 72
silkworms 158
skin of bees 129
slowed-up living 59
smell 74
specialisation 68
spermatophore 52
spermatozoa 52
sponge *14*, 17
sporulation 156, 158
stereotropism 55, 56
sternite 62
stickleback 77
stink-ant 118
Stomochorda 18
Stylops 44
symbiosis 108, 127
synthetic theory 31
tardigrades 56-*58*, 59, 61
tarsi 72
taste 72
taste qualities 73
termites 113, 115, *116*, *117*, 118
territory 84, *84*, 140
thyroxine 35
training procedure 141, 142
transducer 65
transformation displays 78
transposition 96
Trichogramma evanescens 157
triploblastica 17
unexpressed thoughts 92
unicellular organisms 16, 17
vertebrates 18, 19, 20
visual curiosity 98
vomeronasal organ 74
weevil *148*
wolf-spider *26*
wood ants 113, 114, 115, 118, *133*, *134*, 135, *135*, 136, 137
xenogamy 127, 130

Printed in Spain by Talleres Offset Nerecan, San Sebastian—Filmset on the 'Monophoto' by Photoprint Plates Ltd., Basildon, England.

S. C.E.R.T., West Bengal
Library

STATE INSTITUTE F EDU
BANIPUR

THE LIVING UNIVERSE

An Encyclopaedia of the Biological Sciences

The living organism
Life at the molecular level—From cell to organised being—Possibilities and limitations of the living being—The development of the embryo.

The animal world
The singular nature of our kingdom—Animal groups—Sexuality—Animal thought.

The world of plants
How plants colonised the mineral world.

The world of microbes
Bacteria and viruses—Is aseptic life possible?

The human machine: I. the mechanisms
The important inner links—The nervous system—The neuro-physiological bases of mind.

The human machine: II. disorders
The major bacterial diseases—Allergies—Cancer and leukemia.

The human machine: III. adjustments
Deciphering the disorders—The treatment of disease—Pharmacology.

Man of tomorrow
Improving the environment—Improving the species—Grafts and eugenics—Man of the future—Medicine of the future.

NELSON
36 PARK STREET, LONDON W.1